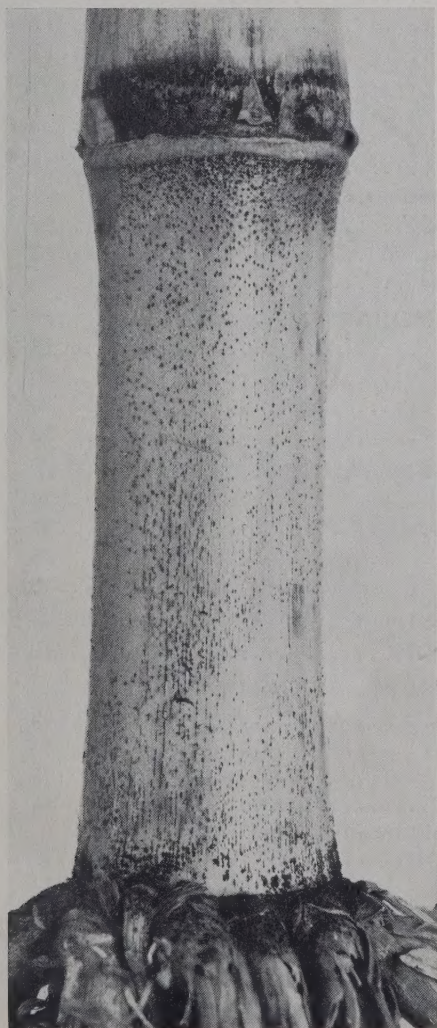
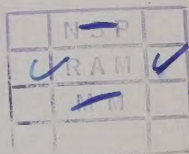


CORNSTALK ROTS IN ILLINOIS

By BENJAMIN KOEHLER



Bulletin 658



UNIVERSITY OF ILLINOIS · AGRICULTURAL EXPERIMENT STATION



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FOREWORD

CORNSTALK ROTS IN ILLINOIS is the third of a series of Illinois Agricultural Experiment Station Bulletins recently published by the author. These bulletins are the culmination of his principal research projects on corn diseases conducted in Illinois over a considerable number of years.

PERICARP INJURIES IN SEED CORN, Bulletin 617, discusses the relation of pericarp injuries to seedling blight resulting from soil-borne organisms. In samples of commercially processed seed corn examined after staining, 50 to nearly 100 percent of the kernels had broken places in the pericarp. These samples had been obtained from many different seedsmen. Moisture content of seed when subjected to mechanical processes, seed maturity, hybrid combination, and methods of handling when processing, all had an effect on the amount of pericarp injury. Seed treatment with a good protective fungicide gave a very significant but not complete control when seed was planted in cool damp soil. Practically all corn belt soil appeared to harbor potential seedling blight organisms, but seed completely free from broken pericarps was found to be practically free from infection during the critical early germination stage. Unbroken seed produced significantly higher yields of grain than did seed with broken pericarps.

CORN EAR ROTS IN ILLINOIS, Bulletin 639, gives descriptions and, for the most part, illustrations of 10 different fungus ear rots occurring in the field and in storage. Yearly variations in ear rot prevalence are given for a period of 36 years. These variations were found to be influenced greatly by differences in rainfall. Results of studies on the effect of husk protection, lodging, cropping sequence, soil fertility, inherent resistance of the inbred or hybrid combination, and other influences are reported. Data from terminal markets and other sources revealed that the average annual loss from corn ear rots in Illinois is about $1\frac{1}{2}$ million dollars. The long-time study also revealed that on the average very little improvement has been made in the inherent resistance to ear rots of the corn grown in Illinois. It was concluded that ear rots occurring in the field can be partially controlled, and that with suitable equipment rots occurring in storage can be controlled completely.

The seedling blights, ear rots, and stalk rots discussed in these three bulletins are by no means the only diseases that affect corn in Illinois or throughout the corn belt. Some other diseases of field corn that are either frequently or occasionally of importance are: smut, Stewart's leaf blight, *Helminthosporium* leaf blights, rust, root rots, and crazy top. Many other corn diseases normally are of no economic importance but under unusual conditions may become prevalent enough to attract attention.

CORNSTALK ROTS IN ILLINOIS

By BENJAMIN KOEHLER, Professor of Plant Pathology

CORNSTALK ROTS are in general the most serious group of diseases of dent corn in Illinois and in the corn belt. The amount of loss varies widely from year to year and in different places. This variation is partly due to weather conditions and to the amount of inoculum carried over from the previous year as well as to differences in cultural practices and in the varieties used. For a time during the development of hybrid corn, standability was considerably improved. In more recent years, however, further improvements in the standability of the corn grown on farms have been minor. Corn breeders have concentrated on higher-yielding hybrids, and agronomists have worked on increasing soil fertility levels, on thicker planting, and on more intensive cropping to corn. Increasing the fertility of soil also increases corn's susceptibility to stalk rot, and thicker planting increases its susceptibility to stalk breaking. Thus on many occasions the gains in inherent resistance to stalk rot have largely been nullified.

This bulletin is concerned with describing the diseases, the amount of rot that occurs, the damage done, the way that the pathogens enter and the diseases develop in the stalk, and the problems relating to the use of artificial inoculation for controlled research. Some of the literature touching on these points is reviewed. Those interested in a description of the pathogens causing stalk rots are referred to Dickson (20)¹ and to the references cited by him.

DESCRIPTIONS OF STALK ROT DISEASES

Diplodia Stalk Rot

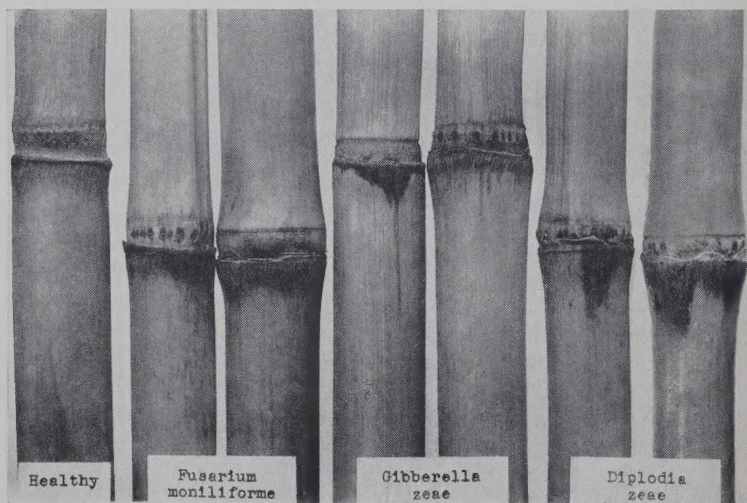
Diplodia zeae (Schw.) Lév. is, on the average, the most common cause of cornstalk rot in Illinois (52). This seems to be true also in states adjacent to the east and west, but in the drier western part of the corn belt, charcoal rot is more damaging (58), while north of the latitude of Chicago and from Ohio eastward, *Gibberella* stalk rot is reported to be more important (6, 19, 68, 75, 104). *D. zeae* is also troublesome as a cause of ear rot of corn but the disease is not systemic, and susceptibility of the stalks is not associated with susceptibility of the ears (31, 42, 50, 55, 103).

¹ Figures in parentheses refer to literature citations on pages 85 to 90.

Diplodia stalk infection is first visible as dark brown lesions extending in either direction from the nodes (Figs. 1, 22-right). These may appear a few weeks after pollination, and by mid-September the darkened areas may extend the length of an internode, or more. This dark color develops only while the fungus is growing in the cortex of green stalks. Usually the fungus soon penetrates into and spreads through the deeper tissues (Fig. 2), causing a softening of the stalks. Stalks generally become more predisposed to infection as the ear grows in size. Plants that do not bear ears do not become susceptible.

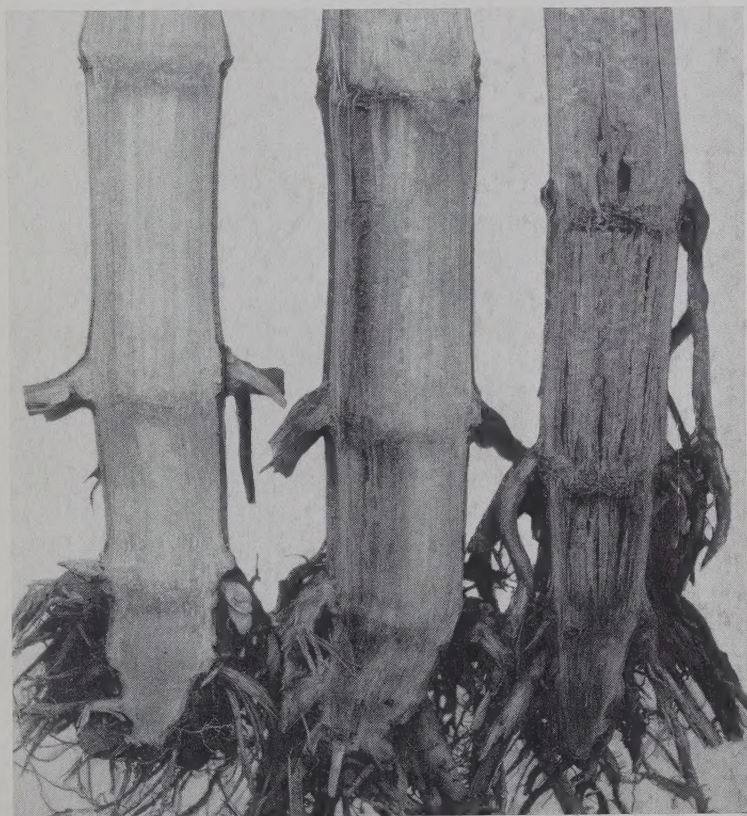
Much of the infection, as observed in Illinois, starts at any of the first three nodes above ground, but it may start also at higher and lower nodes (Table 8). This will be discussed further under the heading of "NATURAL PLACES OF ENTRY OF FUNGI INTO STALKS," page 62.

After the stalk dies as a result of infection, the fungus continues to grow and cause further decay as long as moisture is adequate, but it produces little additional external discoloration. Numerous slightly raised black dots, the spore-bearing bodies, may appear soon after the stalks have died, or their appearance may be delayed until spring. These fruiting structures, called pycnidia, develop just below the surface of infected stalks. As they mature, the beaks break through to the exterior (Figs. 3-left, 4-A). The pycnidia develop only sparsely or



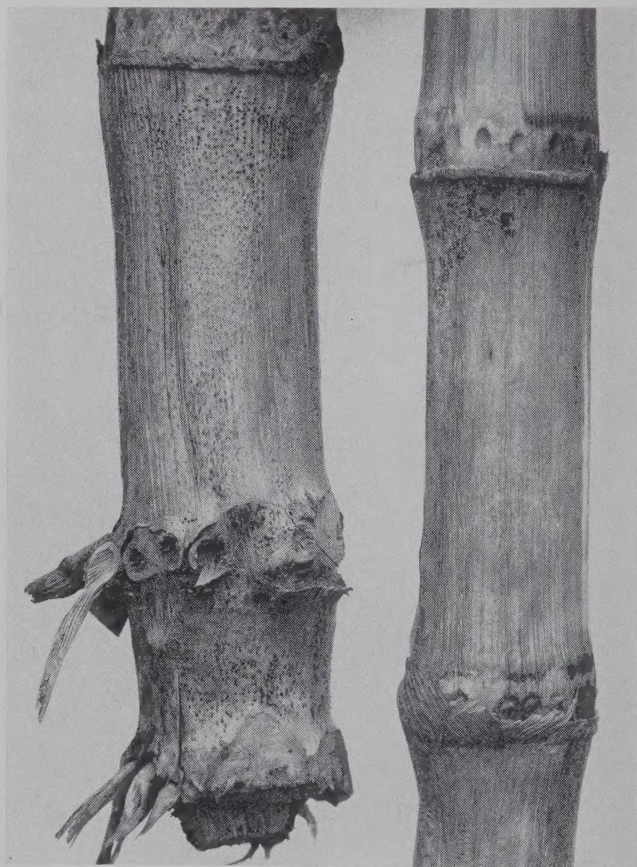
Rots caused by several fungi originating at the bases of leaf sheaths at the nodes of cornstalks. (Fig. 1)

not at all on the darkest lesions but may appear abundantly on adjacent areas. Thousands of tiny two-celled spores are produced in each pycnidium. It is not until these pycnidia develop that the cause of the rot can be identified with assurance in the field. The spores overwinter within the pycnidia in the old cornstalks, and when, under suitable weather conditions, the spores are discharged (Fig. 4-B) in the following August and September, they may cause stalk and ear rot infection in the new crop. So far as known, this fungus attacks only corn.

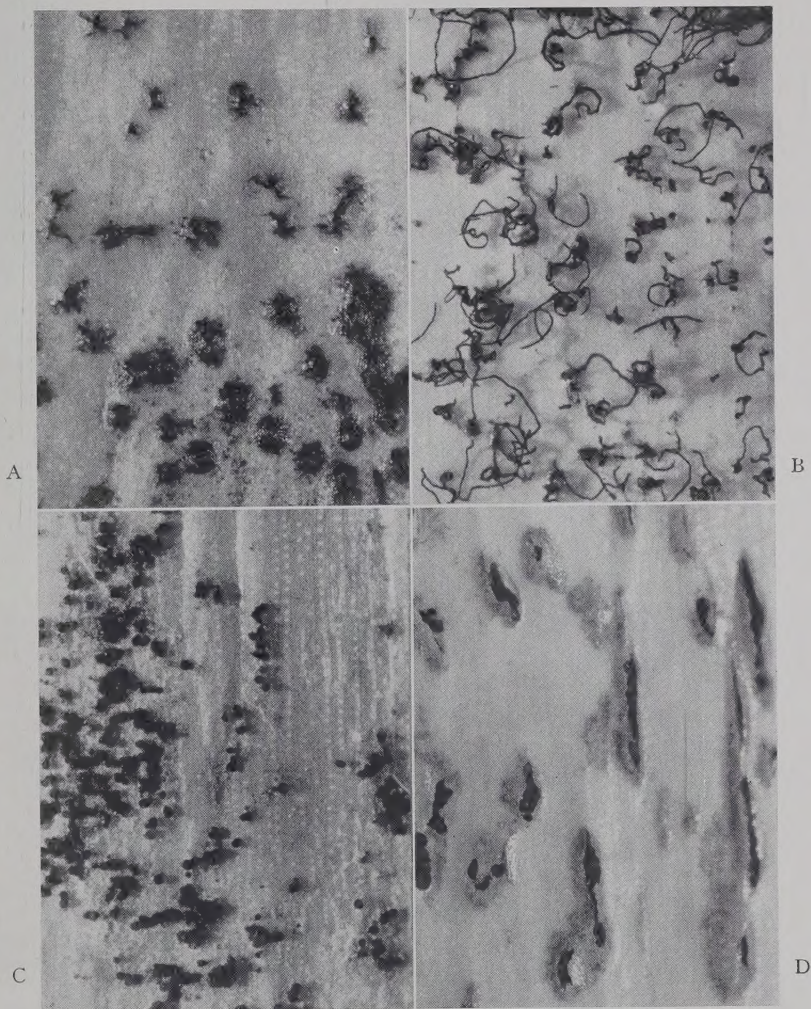


Diplodia stalk rot shown on the interior of split open stalks. Left, healthy stalk from a green plant. Center, green stalk with rot that was progressing rapidly, leaves on the plant were dying giving an appearance similar to frost damage. Right, the stalk as well as leaves was dead. (Fig. 2)

A few plants at various places in a field may die in late August, but most dying from this disease usually does not occur until mid-September. The leaves die first, giving an appearance somewhat similar to that of frost damage. The stalks of such plants usually die 7 to 10 days later. This may result in broken stalks (Fig. 19) and in reductions in yield. In years when stalk rot does not become active until the corn is nearly mature, stalk breaking is the only damage. This, however, can be serious in that the ears can not all be harvested,



Fruiting bodies of cornstalk rot pathogens within which spores are produced. Left, pycnidia of *Diplodia zeae*. Right, jet-black perithecia of *Gibberella zeae*. For enlarged picture, see Fig. 4. (Fig. 3)



Fruiting bodies on cornstalks, enlarged $\times 16$. A, pycnidia of *Diplodia zeae*. These are formed beneath the surface and break through as they develop. B, *Diplodia zeae* pycnidia discharging spores. They emerge in long tendrils consisting of many spores held together by a water-soluble viscid substance. This occurs under damp conditions after the spores have matured. C, perithecia of *Gibberella zeae*. These bodies appear like round black balls on the surface of the cornstalk. D, pycnidia of *Phaeocytospora zeae*. These develop beneath the surface and are nearly black like those of *D. zeae*, but can readily be distinguished from the latter in that most of them are considerably elongated. (Fig. 4)

mechanical pickers become clogged, and ears in contact with the ground may rot.

Conditions that predispose plants to infection by the *Diplodia* stalk rot fungus are: inherent susceptibility; leaf blight; an inadequate supply of potassium in the soil as compared with the amount of nitrogen present; high fertility levels in general; early frost damage; partial defoliation due to chinch bug, grasshopper, or hail, especially if it occurs during August; and sometimes the use of early-maturing varieties. Some stalk rot may possibly arise from seed infection, but ordinarily little seed of good quality is infected with *Diplodia*.

Weather conditions also are important in determining the prevalence of stalk rot. The occurrence of severe infection is dependent on an abundance of viable spores in the air some time during August. Under suitable moisture conditions, mature spores, adhering to each other, ooze out of the pycnidia in long tendrils (Fig. 4-B). After exposure to the atmosphere, the spores separate and are carried considerable distances by the wind (8). Moisture is then required to wash the spores down behind the leaf sheaths (22). Mycelium from the spores may then enter the sheaths and work its way down the vascular bundles into the stalk at the nodes where the sheaths attach to the stalk. Wounds are of little consequence.

Gibberella Stalk Rot

Gibberella zeae (Schw.) Petch frequently causes serious stalk rot damage in Illinois. It is generally the most important cause of corn-stalk rot in the New England, the mid-Atlantic, and the northern corn belt states. In addition, it causes corn ear rot and root rot, but it is not systemic. This fungus also attacks a considerable number of other crops and is important as a cause of wheat and barley scab.

The initial infection of the stalk may begin soon after pollination (Fig. 24). It is revealed by dark lesions that are not easily distinguished from those caused by *Diplodia zeae* (Figs. 1, 5). Sometimes the lesions show concentric rings (Fig. 6), but this is not common. The lesions as seen on the exterior of the stalk sometimes appear slightly more streaked than happens with other infections (Figs. 1, 25, 27). At other times, there is no apparent difference in the external appearance of the lesions until the fungus fruits. When the stalks are split lengthwise after the rot has made considerable progress, a limited amount of pink coloration is likely to be present, but this color does not usually occur throughout the rotted area, nor is it always found. Otherwise the rot in the interior is much like that caused by *Diplodia* (Fig. 2).

This fungus, like *D. zeae*, is best identified by its fruiting bodies, called perithecia. Two kinds of spores are produced, ascospores, which are enclosed within the perithecia, and conidiospores, which are not enclosed. The small, black, spherical perithecia are visible to the

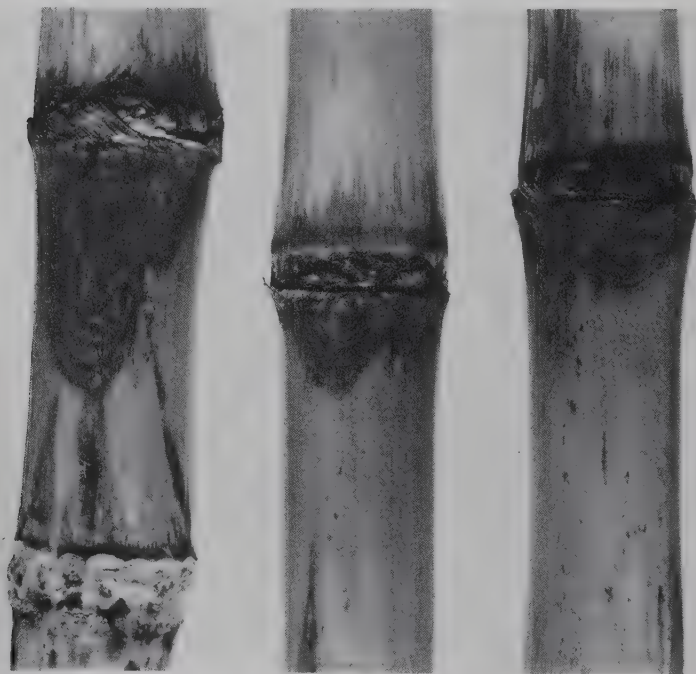


Cornstalks showing discoloration caused by infection with *Gibberella zeae*. The discoloration shown in this picture is a common external appearance and can not be distinguished from discolorations caused by *Diplodia zeae*. In such cases, positive identification requires plating. See also Figs. 6, 25, and 27. (Fig. 5)

naked eye (Fig. 3-right), but their exact shape (Fig. 4-C) can not be seen without a good hand lens. Unlike the fruiting bodies of *Diplodia*, the perithecia are borne on the surface and can be scraped off. The perithecia of *G. zeae* can be distinguished from those of *Gibberella fujikuroi* only by a microscopic examination of the ascospores. However, the perithecial stage of *G. fujikuroi* has not yet been found in any of the numerous microscopic examinations of perithecia collected in Illinois (52).

The perithecia of *G. zeae* do not develop as readily as the pycnidia of *Diplodia*. Occasionally they are numerous in late fall, but sometimes they are sparse even though *Gibberella* stalk rot is abundant. In many cases the ascospores do not mature until the following spring or summer. The spores are distributed by the wind to the succeeding corn crops in the neighborhood.

When stalk rot infection is severe, *Gibberella* seems to cause more breaking down of stalks than *Diplodia* does.



Concentric rings sometimes produced by infection with *Gibberella zeae*.
(Fig. 6)

In general, the conditions that predispose plants to *Diplodia* stalk rot also favor the development of *Gibberella* stalk rot. All corn plants are highly resistant to both until after silking time, and those that bear no ears remain resistant. After silking, different inbreds and hybrids vary widely in their resistance, but in general, although there are exceptions, a given inbred or hybrid is likely to be about as resistant to one of these stalk rots as it is to the other. Usually both fungi are present to some extent and often both occupy the same rotted area. In some years *Gibberella* is the primary cause of stalk rot and in others it is *Diplodia*, indicating that the two diseases vary in their environmental requirements.

Fusarium Stalk Rot

Fusarium moniliforme Sheldon, emend. Snyder and Hansen [*Gibberella fujikuroi* (Saw.) Wr.]¹ is widely distributed throughout the world as a parasite of many crops and is best known in the United States as a cause of corn ear rot or kernel rot. However, it is also commonly isolated from lesions or rotted areas in cornstalks (2, 6, 24, 45, 52, 60, 75, 95) and under some conditions appears to be able to cause the premature death of plants (52). Limber (57) inoculated cornstalks with a strain of *F. moniliforme* and found dark discolorations and streaks within the stalks extending to the third or fourth internode above and below the point of inoculation. The same fungus could in all cases be reisolated from the dark streaks. Koch and Murwin (45) concluded that in Ontario, *F. moniliforme* is a more virulent stalk rot pathogen than *Gibberella zeae*. The symptoms were found to be similar, both causing reddish color in the interior of stalks. Roane (75) reported that in certain years *F. moniliforme* was of major importance as a cornstalk rot pathogen in Virginia. In Illinois, there is little doubt that in cornstalks this fungus is of minor importance compared with *Diplodia zeae* and *G. zeae*.

The lesions caused by *F. moniliforme* on some naturally infected nodes are shown in Fig. 1. The margins of these dark lesions are sometimes indistinct. Such lesions may begin to develop in August but do

¹ The name *Fusarium moniliforme* is used here rather than *Gibberella fujikuroi* because the *Fusarium* spore stage is constantly seen in Illinois, while the *Gibberella* stage has not yet been observed here. This usage is proper according to the international rules for nomenclature (56). The ascigerous or *Gibberella* spore stage is known in the United States, however. It has been reported from Ohio (98), New Jersey (98), and Virginia (75) and has occurred abundantly in Florida (102). No distinction has been made between *F. moniliforme* and *F. moniliforme* var. *subglutinans* (24). The validity of this distinction is still uncertain. Furthermore, good criteria do not exist for distinguishing between these species in routine isolations.

not usually spread very far. They weaken the node and may cause stalk breakage. Lesions caused by *D. zeae* and *G. zeae* on green immature plants usually have a more definite margin and may increase in size until the whole internode is involved.

F. moniliforme attacks the stalks earlier in the season than *D. zeae* or *G. zeae*. In a 2-year study (Fig. 24), nearly 26 percent of the stalks were infected by July 26. Most of these early lesions were below ground, but some were at the node at the soil surface and a few at the next higher node, which bears the main brace roots. How much earlier such lesions may develop was not determined. Even at later dates, *F. moniliforme* was the fungus most frequently isolated at all positions on the stalks but one (Table 8). These experiments were conducted to determine the fungus content of lesions in their early stages at various locations on the stalk. Though *F. moniliforme* was common, it caused only minor damage.

This fungus may penetrate the stalk directly, but its entrance is greatly facilitated by the presence of wounds. It is most often found (Table 8) in lesions or rots which develop after the stalk has been attacked by various insects below ground and by corn borers above. Sometimes internodal growth cracks occur. These also provide ingress for *F. moniliforme*. This was made abundantly clear during the examination of a number of stalks so injured (Fig. 7) which were collected about September 10, 1956. In all cases rot had started on the inner surfaces throughout the length of the cracks. *F. moniliforme* was found by isolation tests to be the predominant fungus in the internal tissues surrounding the cracks. Bacteria also were generally present. Except at the nodes, the more aggressive stalk rot pathogens were not isolated from rot adjoining the cracks.

Little is known about conditions that favor the development of this stalk rot disease. It is similar to some other stalk rot diseases in that considerable moisture is required. In some other respects, however, the governing factors seem to be different from those that influence the development of *Diplodia* and *Gibberella* rot. For example, sap-soluble substances that retarded the growth of *D. zeae* and *G. zeae* had little influence on the growth of *F. moniliforme* (40). Also, stalks are somewhat susceptible to *F. moniliforme* in the pre-pollination period.

Charcoal Rot

Charcoal rot is caused by the fungus *Sclerotium bataticola* Taub. The pycnidial stage of this fungus is called *Macrophomina phaseoli* (Maubl.) Ashby. It has not been observed on corn in Illinois.



Growth cracks in cornstalks. Rot in the interior of stalks around these cracks was caused by *Fusarium moniliforme*.

(Fig. 7)

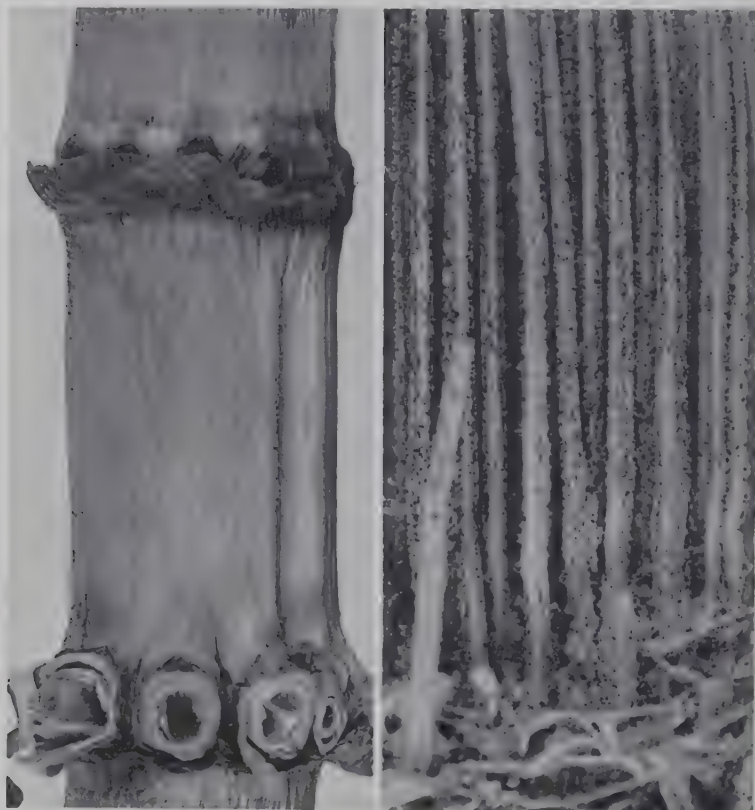
Charcoal rot attacks many crops in various parts of the world. In the United States it appears to be particularly damaging to corn and sorghum in the states from Texas to Nebraska (58, 109) during hot and moderately dry weather. This disease is also damaging to corn in Illinois when similar weather prevails in late summer. The disease was unusually prevalent in the southern half of Illinois in 1953 and 1955.

Stalks become susceptible to this fungus somewhat later than to the other aggressive stalk rot pathogens, but after the rot has started, it progresses rapidly. The disease, as seen in Illinois, is usually limited to the lower 8 to 12 inches of the stalk and to the roots but has been seen as high as 20 inches above ground. In corn, most of the infection appears to arise from below ground, although a case has been seen where only the second internode above ground was rotted.

The surface of badly rotted internodes may partly turn gray. A close inspection of the gray area reveals innumerable tiny black dots, called sclerotia, that show through the epidermis of the stalk. These

are very small but visible to the naked eye. When the stalk is cut or broken open, the interior is seen to be disintegrated, with only the vascular strands remaining intact, and these also are covered with the small black sclerotia (Fig. 8). Sclerotia have a function similar to spores and not only cause new infections but also remain alive through periods of adverse conditions.

Severe cases of charcoal rot cause premature death and broken



Sclerotia of *Sclerotium bataticola* in cornstalks. This disease is known as charcoal rot. Left, surface of stalk, enlarged $\times 1\frac{1}{2}$. The sclerotia are beneath the epidermis but visible to the naked eye. Right, sclerotia on the fibers within the stalk, enlarged $\times 6$. The pith has disintegrated owing to action of the fungus.

(Fig. 8)

stalks. Often these are the first symptoms noted. If a stalk damaged by charcoal rot is cut open, the disease is very easily identified by the black sclerotia which are always present in the interior of rotted stalks. But unless the plants break, or die prematurely, or the gray color appears on the surface of the stalk, much of the rot is unnoticed. Often this fungus appears in conjunction with *Diplodia zeae* or *Gibberella zeae*, and then the rot that is present may be due to the combination of pathogens.

A soil temperature of about 100° F. is most favorable for the development of charcoal rot, but the disease has been reported to develop at a temperature as low as 86° F. (58). Either low soil temperature or high soil moisture prevents charcoal rot of cornstalks. For both of these reasons, this disease is not common in Illinois. Crop rotation is not an effective control, and not much is known about varietal resistance in corn. In irrigated areas, charcoal rot can be controlled by maintaining moist soil.

Bacterial Stalk Rot

A bacterial stalk rot disease occurring in Illinois was described by Burrill (7) in 1889. The rot usually was found on low, fertile ground. The plants were described as becoming stunted and turning yellowish with the rot occurring particularly in the roots and in the lower ends of the stalks. Some of the plants eventually died. That disease is not recognizable now from his description, and several pathogens may have been involved. Rosen (76) described a bacterial root and stalk rot occurring in Arkansas in 1919. In some respects the symptoms described resemble Burrill's description and also leave one in doubt concerning the identity of the disease. Later (77, 78) Rosen made some corrections in the description and gave some additional symptoms, and the cause was ascribed to *Phytomonas dissolvens* Rosen. The description then resembled that of the more recently described Pythium stalk rot disease (see page 19). It was reported as having been observed in nine states. The name of the pathogen was later revised to *Erwinia dissolvens* (Rosen) Burkh.

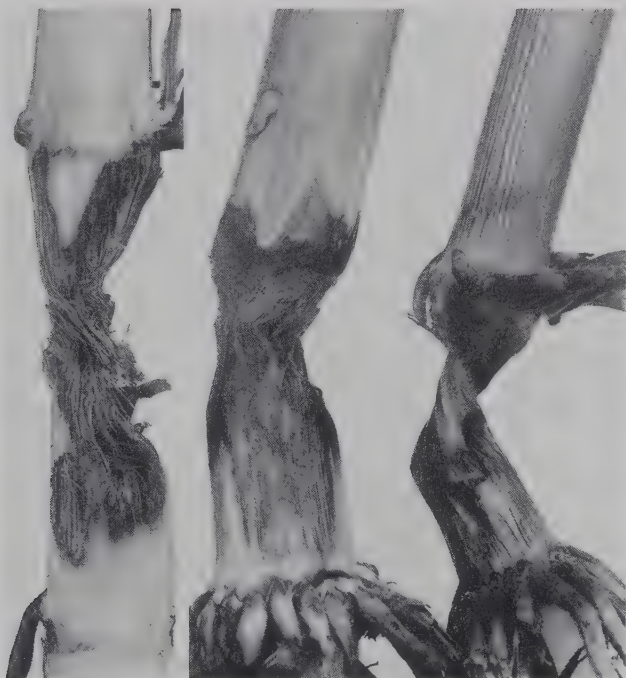
L. R. Tehon listed *P. dissolvens* as having caused a bacterial stalk rot disease which he found in certain counties of southern Illinois in 1921, 1922, and 1923 (96). G. H. Dungan found the disease in two southern Illinois counties in 1922. He sent specimens to H. R. Rosen, who identified them as bacterial stalk rot. In 1936, the writer, accompanied by G. H. Boewe, collected some specimens from a cornfield on river bottom land near Cairo, Illinois. These were sent to H. R.



Bacterial stalk rot caused by *Erwinia dissolvens*. Notice the similarity between this rot and that illustrated in Fig. 10. Unless the *Pythium* mold appears on the surface, which may occur in very humid warm weather, these rots can only be distinguished by a laboratory test, and then only soon after the rot has occurred. (Fig. 9)

Rosen, who identified them as bacterial stalk rot. A considerable number of the plants in this field had rotted near the ground and fallen over. These plants were green and alive even though most of them, it was said, had fallen more than a week earlier. Besides sending specimens to H. R. Rosen, we took photographs (Fig. 9) and brought specimens back to the laboratory at Urbana. Bacteria were present in considerable quantity, and a pure culture was sent to Rosen. He reported the bacteria to be *Erwinia dissolvens*. Since then, stalk rot with the same symptoms has been observed at numerous times in Illinois, but no further specific study of the disease has been made.

An epidemic of bacterial stalk rot occurred in sweet corn in West Virginia in 1930 and in 1931. The causal agent was studied, and a culture was sent to Rosen who identified it as the bacterium originally described by him (90). A bacterial stalk rot resembling the one described by Rosen has also been reported from California (3).



Stalk rot caused by *Pythium butleri*. Left, stalk split open showing the thorough but limited extent of the rot. Center and right, surface appearance. Twisting of the stalk as it falls is common. (Fig. 10)

McKeen (60) reported the occurrence of bacterial stalk rot caused by *E. dissolvens* in Ontario in 1949 during a comparatively hot, humid summer.

Bacterial stalk rot has primarily occurred in Illinois on bottom land, some of it subject to flooding, and also, but to a lesser extent, on flat prairie land. Damp hot weather is required. Thus the disease has been found mostly in the southern half of Illinois (5) in years when weather conditions were favorable for its development.

Pythium Stalk Rot

Pythium butleri Subr. may cause a stalk rot of corn during hot damp weather. It was first identified in Maryland in 1940 (25), in Virginia in 1941 (25), in Indiana and Kentucky in 1949 (99, 101),

and also in Illinois in 1952. This fungus attacks corn in the pre- as well as the post-tasseling period. Plants attacked by *Pythium* and bacterial stalk rot fall to the ground in midsummer. This is much earlier than when lodging is caused by other stalk rot diseases. In contrast to most previously discussed stalk rot diseases, susceptibility does not increase with advance in maturity of the plants. The disease does not cause stunting. It attacks thrifty plants as readily as others, causing them to fall quickly, and the disease usually stops its activity as suddenly as it starts.

Usually only one internode, or a part of an internode, within one foot of the ground is involved (Fig. 10). The rot works quickly through the stalk but is very limited in its vertical progress. The outer rind (cortex), as well as the rest of the stem, rots and becomes soft. Only the vascular strands continue to function. The plants soon fall but remain green and turgid for several days or longer. Elliott (25) observed a plant to collapse four days after artificial inoculation. As the plants fall, they usually twist so that the vascular strands, which are about all that is left in the rotted areas, become spirally twisted.

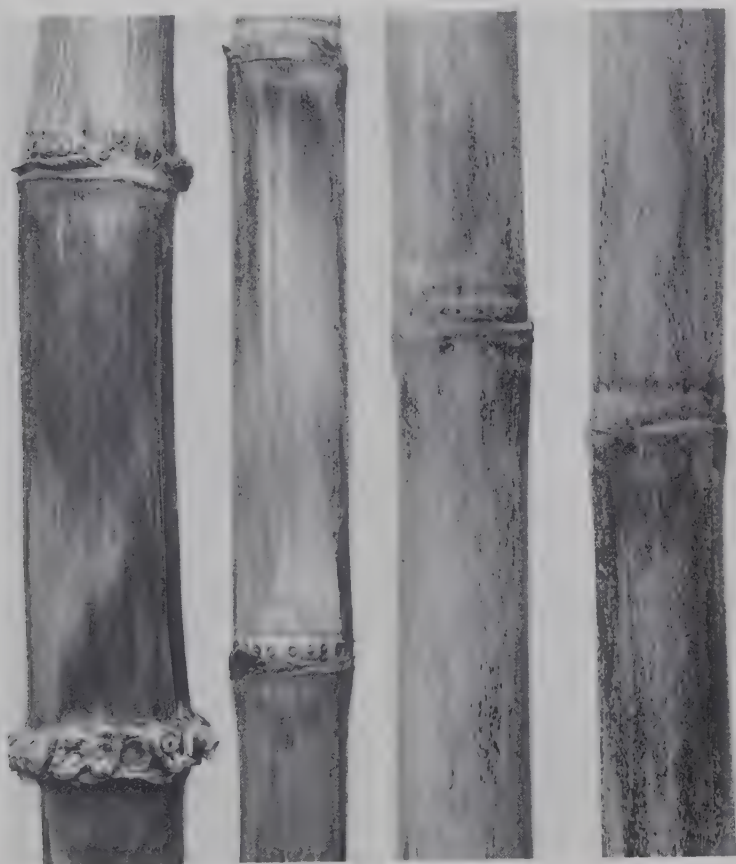
There are differences in the susceptibility of different inbreds (25) and hybrids (101) to *Pythium* stalk rot. However, as the disease develops only when the weather is damp and daily temperatures reach 90° F. or higher for a number of days, it seldom occurs in Illinois.

It seems peculiar that *Pythium* stalk rot and bacterial stalk rot should have apparently identical symptoms. This coincidence merits further study. No other means of identification are known to the author excepting those of making isolations or of observing *P. butleri* actually present on the infected parts. Furthermore, according to Elliott (25), results from isolation attempts may not be valid unless made while or very soon after the disease has been active.

Nigrospora Stalk Infection

The fungus *Nigrospora oryzae* (Berk. and Br.) Petch is better known and is more important as a cause of corn ear rot (50) than as a cause of stalk rot. In Illinois, lesions on the stalks commonly appear as the crop approaches maturity, although in Iowa some infections in the first and third nodes above ground were reported as having occurred prior to silking time (23). The writer has seldom isolated this fungus from the stalks of actively growing plants, except in association with more virulent pathogens (Fig. 18-B). It has been reported that a temporary exposure to cold temperatures makes the stalks more susceptible to attack by *N. oryzae* (85).

As the stalks approach maturity, they may become more or less generally infected on a number of the lower internodes. The lesions are usually very superficial, but occasionally the fungus can be isolated from deeper tissues. The infection enters through the stalk surface of the internodes, probably by means of the stomata. The cases observed have seldom started at a node. The lesions are primarily dark



Surface discolorations on the lower part of cornstalks caused by *Nigrospora oryzae*. Sometimes the discolorations are fairly general as at the left, at other times, they are speckled as on the two stalks to the right. Such lesions have been found only late in the growing season. (Fig. 11)

gray to blackish but often have a slight bluish tinge. The discoloration is shallow and may appear as many separate, tiny blotches (Fig. 11, the two stalks at the right) or as continuous, larger, irregular blotches. *N. oryzae* fruits in abundance on these lesions if such internodes are washed well in tap water and placed in a moist chamber in which the air is kept slightly below saturation.

There is no doubt that this fungus may be damaging to corn ears but, according to observations by the writer, as far as cornstalks are concerned, the infection ordinarily comes too late and is too shallow to be of much importance.

Phaeocytospora stalk infection

Phaeocytospora zeae Stout (92) is frequently found fruiting near the ground on maturing cornstalks. The pycnidia form beneath the surface and break through to the exterior when they become mature. Superficially they resemble *Diplodia* pycnidia except that they are elongated instead of round and that the opening through the surface of the stalk is a short to long slit (Fig. 4-D). The pycnidia have been seen as high as 8 inches above the soil, but usually they are found lower on the stalk and may occur on the first internode below ground, on brace roots, and on roots at the ground level. This fungus has been isolated from mature, rot-damaged roots, and under experimental conditions has caused a root rot of young corn plants (15).

It is not known how much damage this fungus does to Illinois corn. However, stalk infection is widespread over the state, and some of the disease can be readily found each year (52). This fungus has been isolated from lesions on green stalks (Table 8), sometimes as early as August 22.

In culture, the fungus has some resemblance to *Diplodia zeae* (Fig. 18-D), but its growth is a little slower and its surface texture is slightly different. Some *Phaeocytospora* cultures on potato-dextrose agar develop a pale pinkish color on the reverse side, but this is not universal. As there are variations in the appearance of both *D. zeae* and *P. zeae* cultures, a few of them practically intergrade. *P. zeae* is easily identified by the spores produced on potato-dextrose agar slants in about two weeks. These spores are nonseptate, a little shorter than those of *D. zeae*, dusky brown in color, and shaped like pumpkin seeds.

P. zeae appears to have been reported only from Illinois and France (64). In France it was described as infecting the basal part of cornstalks. The writer has not seen infected plant specimens from France, but he has received pycnidia with viable spores. These spores

appeared to be correct for *P. zeae*, and the growth of the fungus on agar medium also produced typical cultural characteristics including the pinkish color in the agar.

Pyrenochaeta Stalk Infection

Pyrenochaeta terrestris (Hansen) Gorenz, Walker, and Larson is well known as a cause of pink root rot of onions and of a mild root rot of many cereals and grasses (89). Johann (39) reported finding this fungus in reddish, diseased mature roots of corn. More recent experiments have definitely established that this fungus can cause a red root rot of corn (15).

P. terrestris occasionally has been isolated at or above the soil surface from stalks collected from late August to late September in Illinois (52). Further detailed studies (Table 8) show that this fungus commonly infects the basal part of the stalk, primarily the part below the soil surface. How soon lesions start to appear was not determined; however, they were common by July 26, which was before tasseling time, and continued to increase in size and number thereafter.

The lesions below the soil surface appeared as dark brown blotches. Many occurred on internodes and appeared to have started independently of roots or of insect attack (Fig. 12-center and right). These lesions were very shallow, not over 1/16 of an inch deep and usually less. No pink color was associated with any of the lesions on green stalks up to September 20. At later dates a pink coloring, which was more widely spread than the dark blotches, sometimes was common in the outer rind of the stalk at the lower end, and *P. terrestris* frequently has been isolated from these reddish areas.

Even though this fungus is able to infect corn plants prior to as well as after tasseling, the infection is believed to be usually of little or no economic importance because the lesions are generally only superficial.

Stewart's Disease Stalk Infection

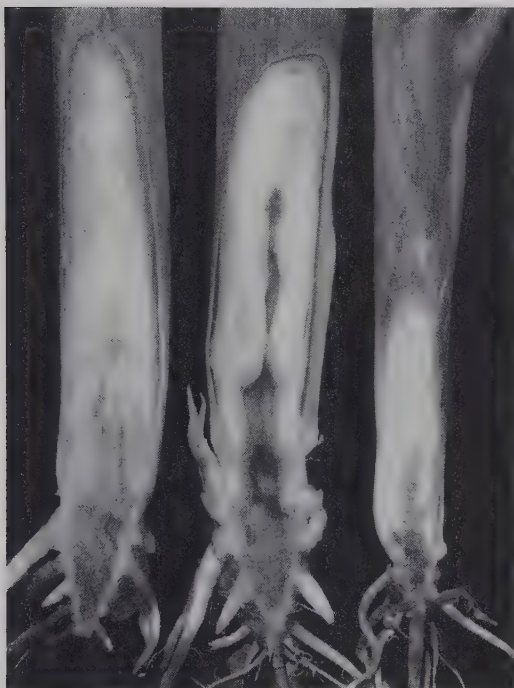
Stewart's disease (bacterial wilt), caused by *Bacterium stewartii*, E. F. Sm., is best known as a wilt and blight disease of sweet corn. In dent corn grown in the central part of the corn belt, it is chiefly a leaf blight. However, in very susceptible dent corn inbreds or hybrids, if infection occurs in the seedling or young plant stage, the disease may become systemic and cause stalk cavities. There are no prominent wilt symptoms in dent corn, and so for this crop the name bacterial wilt appears to be improper.



Left, top, a lesion caused by *Gibberella zeae* originating at the junction of a brace root with the stalk. Below is a rot within the stalk caused by *Diplodia zeae*, which was continuous with a rotted root. Center, top, shows another example of *G. zeae* lesions at the brace roots. Center and right, dark lesions on internodes below the soil surface were caused by *Pyrenochaeta terrestris*. (Fig. 12)

The lower end of the stem may start becoming hollow (Fig. 13) when the stem is only a few inches above ground (plants about knee high). The cavities, which are caused by the collapse of tissue, are yellowish to medium brown at first and finally turn dark brown. Such cavities may also occur in full-grown plants (Fig. 14). Usually there is enough healthy peripheral tissue left so that the plants do not die early, but leaf blighting may take place.

This disease is identified by the yellow bacterial slime that oozes slightly from freshly cut vascular bundles of diseased stalks, particularly when the plants are turgid. At other times, bacterial slime can be forced from the bundles by pressure with the fingers.



Stalk damage caused by *Bacterium stewartii*. A shrinking and disintegration of the central tissues at the lower end of stalks of young plants of susceptible varieties of sweet or dent corn sometimes is associated with Stewart's disease (bacterial wilt). The plants illustrated were susceptible dent corn inbreds. (Fig. 13)

The bacteria that cause Stewart's disease are primarily carried through the winter within the bodies of corn flea beetles, and these insects are also responsible for spreading the disease during the summer. The disease occurs only after mild winters. Severe epidemics may occur only after conditions have been favorable for disease development for several successive years.

Stewart's disease is controlled through resistant varieties. Corn inbreds differ considerably in susceptibility, and there is an association between resistance to Stewart's disease and resistance to Northern leaf blight (49). A number of inbreds resistant to both diseases are available.



Stalk disintegrations caused by Stewart's disease in a susceptible variety of dent corn. Photographed in early September. Healthy stalk at the left. (Fig. 14)

Other Stalk Rots or Infections

A serious root and stalk rot disease has been reported from Ontario (60, 105). The symptoms described and illustrated do not closely resemble any disease observed by the writer in Illinois, although this does not prove its absence here. The disease starts as a root rot and moves up into the stalks. The exact cause has not been determined.



Lower ends of cornstalks split open on September 20. A, rot from which a species of *Pythium* was isolated. B, dark rot near surface, above ground, caused by *Diplodia zeae*; below ground, a dark fungus was isolated but not identified. C, only *Cephalosporium acremonium* was found in the central area of this stalk. *Pyrenochaeta terrestris* occurred near the surface. D, *Gibberella zeae* and *D. zeae* both apparently started a rot at the node at the soil surface labeled, a, but the infection did not extend to the lowest end of the stalk. *Fusarium moniliforme* occurred in all isolations made throughout the area shown of that stalk. (Fig. 15)

Occasionally *Pythium* species other than *P. butleri*, discussed earlier, have been found in cornstalks in Illinois. At all dates some samples taken for the experiment whose results are reported in Table 8 contained a few instances of a *Pythium* provisionally identified as *P. graminicola* Šubr. It was isolated from the lower end of the rotted stalks (Fig. 15-A). In another study previously reported (52) *Gibberella zeae* and what appeared to be a *Pythium* species were sometimes associated in rot damaged areas one to several internodes above ground. Such disorganized tissues were usually wetter than others. Some parts of the rotted areas contained spores characteristic of *Pythium* oospores. However all attempts at obtaining cultures from these oospores failed. *Pythium graminicola* was isolated from above-ground nodes of cornstalks in Iowa (83).

A bacterial leaf blight and stalk rot of corn caused by *Pseudomonas alboprecipitans* Rosen has been reported (41) as occurring in a number of southern and central states. This disease causes long, narrow, buff-colored stripes on the leaves. The leaf symptoms are more common and always precede the stalk rot. After the leaf tissue in the stripes has died, the leaves become shredded in stormy weather. The stalk rot phase has been reported as having been found only above the node that bears the ear. The interior had rotted and turned black, leaving only the vascular bundles. The tops then usually broke over.

In Illinois, the leaf blight phase of the disease was observed on some proprietary corn inbreds in Douglas and Bureau counties in 1951. It occurred most strikingly on the leaves below the ears. The stalk rot phase was not seen.

Pure cultures of *Cephalosporium acremonium* Corda have often been isolated from diseased areas in cornstalks (Table 8). As far as stalk rot is concerned, it appears to be an active parasite but a weak pathogen.

Helminthosporium species occasionally have been isolated from lesions on green (Table 8) and dead stalks (52). A number of isolates were sent to A. J. Ullstrup for identification, and the majority were determined to be *H. carbonum*. A similar fungus, perhaps the same species, occurring on nodes of cornstalks, was collected from widely separated places in Illinois in 1926 by Stout (92). Apparently, this fungus is of little economic importance as a stalk rot pathogen.

GENERAL METHODS OF EXPERIMENTATION

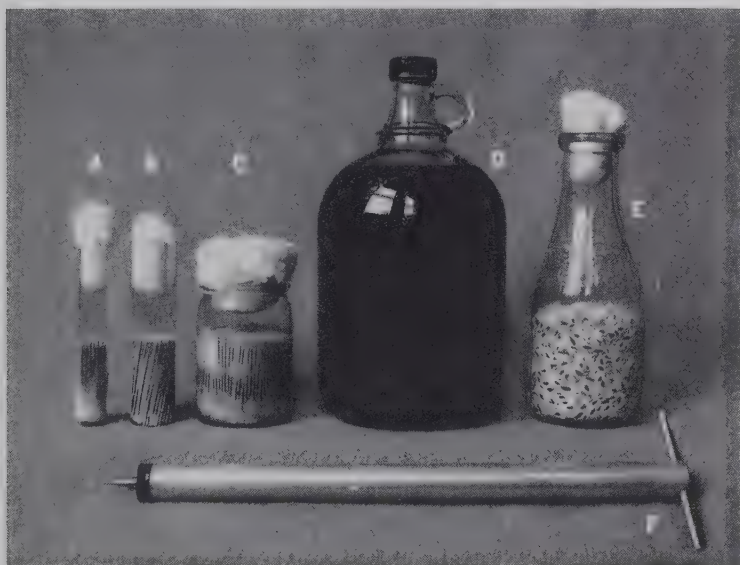
Field Plots

Stalk rot data on natural infection in inbreds and hybrids have been obtained mostly from plots on the Agronomy South Farm, Urbana, and from commercial hybrids in some of the standard hybrid corn tests conducted annually for many years in various parts of the state by the Agronomy Department (12, 13, 21, 70, 71, 72, 73). Data on disease incidence were obtained from the latter tests only when more than an average amount of stalk rot occurred. Such records were usually made from September 15 to 20. The plots were usually 10 to 16 hills in size and were replicated 4 to 10 times.

Stalk inoculation experiments were conducted only at Urbana. The plots were overplanted and later thinned to the desired stand. Each plot was 16 or more plants in size and was replicated 4 times. Various inoculation techniques, described later, were used. The results were usually recorded six weeks after the inoculations had been made.

Preparation of Inoculum

Diplodia spores were produced in abundance on sterilized cooked oats in one-quart milk bottles. The production of *Diplodia* spores and the preparation of spore suspensions used as inoculum have been described in Illinois Bulletin 639 (50), and the products are illustrated in Fig. 16-D, E. Cultures of *Diplodia zeae* and *Gibberella zeae* were also prepared on toothpicks as originally described by Young (107). This process, as used by the writer, was as follows: Round toothpicks were boiled for several minutes in a quantity of water and were then poured out in a thin layer on a large fine screen to dry. The following day they were placed in large-diameter culture tubes or larger vessels, allowing enough space for the toothpicks to swell and still be removed easily when used in the field. Three sizes of containers are shown in Fig. 16-A, B, C. These hold 50, 130, and 700 round toothpicks, respectively. A is an ordinary 1 x 6 inch bacteriological culture tube with



Inoculum and inoculator used for making artificial inoculations. A, B, C, three sizes of containers used at various times for preparing fungus cultures on toothpicks (see text). D, one gallon of dark-colored spore suspensions prepared from one mature culture of *Diplodia zeae* grown on cooked oats in a one-quart milk bottle as shown at E. F, inoculator used for injecting spore suspensions into cornstalks. (Fig. 16)

rounded bottom, B is a $1\frac{1}{2} \times 6$ inch Pyrex vessel with flat bottom, made to order, and C is an ordinary one-pint Mason jar.

The toothpicks were well covered with potato-dextrose broth (200 grams diced potatoes per liter of water kept at boiling temperature in a steamer for one hour, filtered, and 20 grams dextrose added), and the open tubes were autoclaved at 15 pounds pressure for one-half hour. The tubes with contents were then allowed to stand overnight. The following day, the broth was poured off, but not drained, so that a little broth remained in the tubes. The mouths of the tubes were then cleaned with damp cheesecloth, plugged with long fiber, non-absorbent cotton, and autoclaved again. When the tubes were cool, a pure culture of the desired fungus was introduced under aseptic conditions into about the center of the mass of toothpicks.

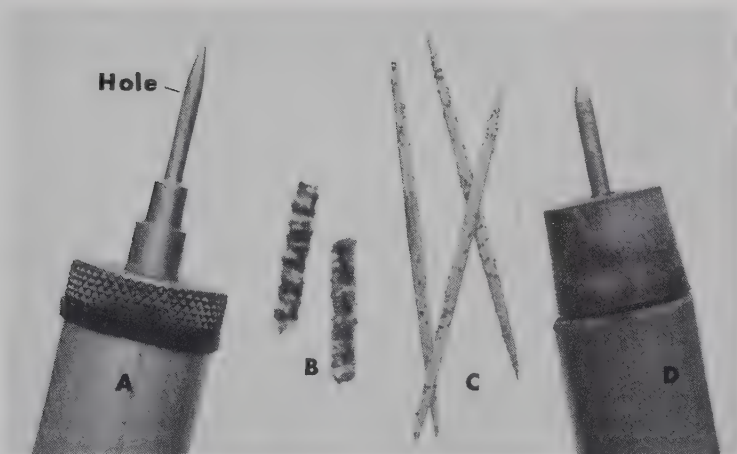
Cultures of *Gibberella* were also prepared on cooked oat kernels for certain tests. The method of preparing these cultures has been described (50).

Any *D. zeae* cultures that sporulated well were found to be satisfactory for inoculation purposes. *G. zeae* cultures, however, varied more in pathogenicity. This character also has been observed by others (106).

Inoculation Methods

Inoculations with *Diplodia zeae* were made most quickly and very satisfactorily with a spore suspension and an inoculator (Figs. 16-F, 17-A). One gallon of dark-colored spore suspension (Fig. 16-D) containing about 8 million spores per ml. was made up from a *D. zeae* culture grown on oat kernels in a one-quart milk bottle. The inoculator has been described (43, 46). One important feature of this inoculator is that the needle has holes on the sides rather than at the end. Therefore, the holes seldom become clogged. This idea is credited to Ivanoff (37). The other very important detail is a short, strong, stainless steel needle that will not become damaged in use (Fig. 17-A). This needle was designed by R. W. Jugenheimer, Professor of Plant Genetics, University of Illinois. The needle, made to order, is $\frac{1}{8}$ inch in diameter and 1 inch long from the point to the shoulder. The cross hole is 0.02 inch in diameter and $\frac{3}{8}$ of an inch back from the point. It is made with a No. 76 drill. The longitudinal hole in the shank of the needle is slightly larger. The shoulder not only reinforces the needle but acts as a depth gauge when inoculations are being made.

The needle screws into an adapter which in turn screws into an aluminum cylinder 16 inches long. The other end is closed and provided with a cross handle. The inoculum escapes from the inoculator



Apparatus and materials for making cornstalk inoculations to facilitate selection for resistance. A, needle end of the inoculator (see Fig. 16). B, pieces of pipestem cleaners which were soaked in a spore suspension just before using. C, toothpicks covered with a *Diplodia* growth, including pycnidia. D, a punch for making holes in stalks for inserting pipestem cleaners or toothpicks. (Fig. 17)

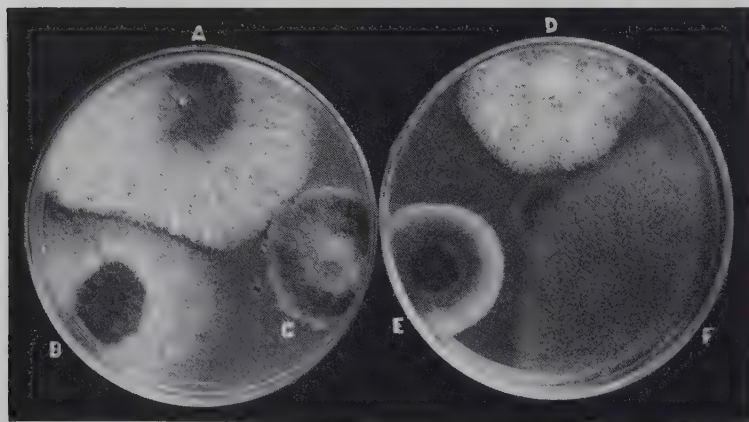
by the force of gravity and of momentum. The inoculator does not have a piston. The air valve used in early models was also found to be unnecessary as the back and forth motion of the inoculator when in use allows adequate air to enter through the needle. In use the inoculator is held at an angle of about 20 degrees from the horizontal. The process is rapid because each inoculation is almost instantaneous and the stalks can thus be inoculated in quick succession. One loading of this instrument holds $4\frac{1}{2}$ ounces of spore suspension, which is sufficient to inoculate about 300 plants. A surplus of suspension is delivered at every jab.

For making inoculations with toothpick cultures, it is first necessary to punch a suitable hole into the stalk. Such a punch was made from an 8-penny common nail (Fig. 17-D). Experiments were made also with 1-inch lengths of pipestem cleaners that had been boiled in water, dried, and soaked in a spore or fragmented mycelial suspension. This method has been described by Wernham (103). A punch made from a 10-penny common nail was used for providing an opening for insertion of the pipestem cleaners.

Various methods for measuring the amount of infection or rot that results from artificial inoculation were tried and compared. The details about these methods will be discussed under the appropriate headings when the determination of the results from artificially caused infection is taken up.

Fungus Identification

Fungi were isolated and identified during the early stages of infection by means of the plating method. Stalks were cut off about 18 to 24 inches above the soil, and at or a little below the soil level, or the entire lower end of the stalk was removed from the soil, depending on the type of experiment. The leaves were then removed and all roots cut off close to the stalk with pruning shears (Figs. 12, 26). The stalks were then washed with a brush under running water, and stood on end to drain. Next, they were either swabbed with mercuric chloride 1:1000 or submerged for 5 minutes in Clorox (5.25 percent sodium hypochlorite) diluted 1:20. Three discolored areas per stalk were usually selected for plating in petri dishes (Fig. 18). When infected tissue was plated, a shaving was first cut off with a flamed scalpel and discarded. Then a piece was taken from the area thus exposed and was transferred to some acidified or nonacidified potato-dextrose agar or water agar. Where it seemed advisable, the stalks



Fungus cultures grown out of fragments of diseased cornstalks plated on potato-dextrose agar. A, *Diplodia zeae* and (dark) *Gibberella zeae*. B, *Nigrospora oryzae* and *Gibberella zeae*. C, *Gibberella zeae*. D, *Phaeocysto-sporella zeae*. E, *Helminthosporium* sp. F, *Sclerotium bataticola*. (Fig. 18)

were split open (Fig. 15) and the pieces to be plated were taken from the interior. This was done consistently when isolating the fungi which caused infection around the tunnels made by corn borers.

The plates were incubated at room temperature for five days, after which the isolates were identified, except for some fungi that required more time before identification could be made. A small percentage of the isolates could not be identified. Sometimes two or more fungi (Fig. 18) originated from a very small piece of stalk. *Diplodia zeae* and *Gibberella zeae* were often found to be closely associated, as reported by Michaelson (66).

After the corn had matured, the fungi causing stalk rot often could be identified in the field, but it was sometimes necessary to cut the stalks open. *Sclerotium bataticola* can always be identified at that stage by the abundant production of sclerotia (Fig. 8), and *D. zeae* frequently produces pycnidia (Figs. 3, 4). *G. zeae* is less often characterized by the presence of fruiting bodies at harvest time, but it frequently can be identified by the lesions on the exterior (Figs. 1, 5, 6, 25, 27) along with some pink coloration in the interior of the stalk. These symptoms usually give a general idea of the cause of rots at harvest time, but some stalks have rots that can not be identified without plating.

DETERMINATION OF STALK ROT PREVALENCE

There is no entirely satisfactory method for determining stalk rot prevalence. Practically all mature stalks are infected to some extent from natural causes. The lesions are most numerous at the lower end of the stalks where they are hard to see and difficult to measure or to estimate. Sometimes the results from the rot, such as stalk breaking or dead plants, are recorded rather than the amount of rot.

Some plants usually escape natural infection to a greater extent than others. The amount of rot may vary considerably in different parts of the same field and may even differ greatly among plants in the same hill. It is therefore important that considerable numbers of plants be examined and experimental plots be well replicated. Furthermore, obtaining reasonably accurate data on the cause of the rot requires a great deal of work, particularly if a considerable number of hybrids or inbreds are involved. To circumvent these difficulties, many investigators have resorted to measuring the extent of rot resulting from artificial inoculation and have ignored whatever natural infection may be present. When stalks are split open, the spread of rot from

inoculation can usually be distinguished from that arising from natural infection, particularly when the readings are made early—about 4 weeks after silking—or before premature dying takes place. Artificial inoculation has the advantages that the cause of the rot is known and that the extent of the rot can be estimated reasonably well, but this method also poses some problems. These will be discussed under the section on artificial inoculation.

Prematurely Dead Plants

Premature death is one of the important and deleterious effects of stalk rot, and the number of dead plants in a given plot can be recorded quickly and accurately. A record of prematurely dead plants, when it can be used, is believed to be generally the best indirect measure of the comparative amount of stalk rot damage present. However, because the actual percent of prematurely dead plants changes from day to day, it is suitable for comparative data within a particular test

Table 1.—Stalk Rot Severity in Nine Single Crosses Six Weeks After Silking (Rot Caused by Natural Infection or by Artificial Inoculation With the Toothpick Method at Silking Time) Urbana, Illinois, 1957

Hybrid (arranged in order of time of silking)	Average number of internodes rotted per stalk as a result of inoculation ^a			Percent of prematurely dead plants following inoculation ^b			Average number of diseased nodes per stalk from natural infection in untreated stalks ^c	
	Check ^d	<i>Gibberella</i> <i>zeae</i>	<i>Diplodia</i> <i>zeae</i>	Check	<i>Gibberella</i> <i>zeae</i>	<i>Diplodia</i> <i>zeae</i>	<i>Gibberella</i> <i>zeae</i>	<i>Diplodia</i> <i>zeae</i>
	A	B	C	D	E	F	G	H
187-2 x 4-8.....	.36	.83	1.22	4.0	4.7	17.6	2.9	.15
Hy2 x R4.....	.25	.88	1.19	4.0	4.2	14.5	2.7	.24
Hy2 x Oh45.....	.40	.90	1.38	0	0	8.5	2.7	.25
Hy2 x B14.....	.35	.82	1.15	3.1	2.7	9.9	1.9	.22
Hy2 x C103.....	.38	.82	1.19	5.7	10.9	17.3	2.7	.08
C103 x B14.....	.19	.56	1.11	1.6	1.7	6.7	2.4	.08
Oh7 x P8.....	.29	.77	1.39	7.8	10.9	42.2	2.8	.36
38-11 x K201.....	.55	1.07	1.57	0	3.3	8.8	1.3	0
L317 x Kys.....	.66	1.14	1.46	19.0	27.2	36.0	3.1	.21
Correlation coefficients, each based on 36 observations								
Column A.....		.75**	.30	.37*	.48**	.30	.03	.07
Column B.....	.75**		.33*	.55**	.57**	.45**	.19	.03
Column C.....	.30	.33*		.34*	.36*	.70**	.35*	.33*
Column D.....	.37*	.55**	.34*		.91**	.79**	.52**	.26
Column E.....	.48**	.57**	.36*	.91**		.78**	.55**	.20
Column F.....	.30	.45**	.70**	.79**	.78**		.63**	.43**
Column G.....	.03	.19	.35*	.52**	.55**	.63**		.42**
Column H.....	.07	.03	.33*	.26	.20	.43**	.42**	

^a Differences in these 3 columns are highly significant for hybrids and organisms used for inoculation, as well as for the interaction between them.

^b Differences are significant for hybrids and organisms, but not for the interaction between them.

^c Differences are significant for hybrids, organisms, and interaction.

^d Sterile toothpicks were inserted into the internodes of these check plants in the same manner as in the toothpick inoculations used for *G. zeae* and *D. zeae*.

* Significant at the 5-percent level.

** Significant at the 1-percent level.

only. In Iowa (81), a significant correlation was obtained between premature dying of corn from natural causes and the spread of rot from stalk inoculations with *Diplodia zeae*. In Illinois (Table 1), a high correlation was obtained between premature dying and both the number of diseased nodes per stalk resulting from natural infection and the extent of rot which results from artificial inoculation with *D. zeae* and *G. zeae*.

In rating many hybrids for stalk rot (12, 13, 21, 71, 72, 73) in different years, all the data, except for two tests, were based on premature dying. The dependability of this method is attested by the high correlations obtained from data gathered over a period of years and from different locations (Table 2). Only in the 1951 test at Sullivan and the 1953 test at Galesburg was another method — stalk

Table 2.—Correlation of Stalk Rot Prevalence of the Same Hybrids at the Same Location in Two Different Years, and at Two Locations in the Same Year

Year	Number of hybrids	Location	Stalk rot prevalence ^a			Correlation coefficient for each pair
			Highest	Lowest	Average of all entries	
			<i>perct.</i>	<i>perct.</i>	<i>perct.</i>	
Interannual correlations						
1938.....	36	Sullivan	87	10	47}	+.70**
1939.....	36	Sullivan	57	9	36}	
1950.....	44	Sheldon	47	3	13}	+.67**
1951.....	44	Sheldon	38	6	17}	
1951.....	30	Galesburg	33	5	12}	+.52**
1953.....	30	Galesburg	24	2	9}	
Interlocation correlations						
1938.....	32	Sullivan	87	17	59}	+.84**
1938.....	32	Albion	86	28	66}	
1939.....	23	Cambridge	61	1	14}	+.52*
1939.....	23	Littleton	75	10	39}	
1941.....	22	Mt. Pulaski	34	1	12}	+.79**
1941.....	22	Sullivan	20	1	11}	
1951.....	40	Galesburg	26	3	12}	+.84**
1951.....	40	Sheldon	37	4	16}	
1951.....	31	Galesburg	29	3	12}	+.75**
1951.....	31	Sullivan	41	4	18}	
1951.....	33	Sheldon	34	5	15}	+.74**
1951.....	33	Sullivan	41	4	16}	

^a Prevalence was based on the percentage of prematurely dead plants except for the tests at Sullivan in 1951 and at Galesburg in 1953 when stalk discoloration was used (see text).

* Significant at the 5-percent level.

** Significant at the 1-percent level.

discoloration — used. This was necessary because of severe northern leaf blight at Sullivan and heavy corn borer damage at Galesburg in those years. The ratings of hybrids by the stalk discoloration method correlated highly with ratings for the same hybrids obtained on the basis of prematurely dead plants in other years (Table 2).

Premature death results in yield reduction and often in broken stalks. Prematurely dead plants are numerous enough to serve as a basis for measuring the incidence of rot only if the rot is epidemic. The epidemic may be either natural or induced. When artificially induced, multiple inoculations per stalk with *D. zeae* are most likely to give the desired effect (Table 3). Inoculations with *G. zeae* have usually resulted in less premature dying (Tables 1, 6, 11).

A record of premature dying is of value for measuring stalk rot damage only if (a) stalk rot is the primary cause of the condition, and (b) the hybrids or inbreds to be compared are of the same maturity range. If they are not, then compensation for differences in maturity must be made. When silking dates have differed, an attempt at compensating for differences in maturity has been made by making the records at the same number of days after silking (Table 1).

Data on premature death should be taken before the leaves die as a result of maturity. The method is useless when serious leaf blight damage or drouth occurs. When conditions are satisfactory, the data may be based on the number of plants with dead leaves, or ten days later, data may be taken nearly as accurately by ignoring the leaves and counting the number of dead stalks. To count the dead stalks, it is necessary to remove some of the leaf sheaths below the ear and to observe whether the stalk is bright green or blanched. Jugenheimer (42) rated plants as (1) green plants, (2) leaves partly dead, and (3) leaves and stalks dead.

Table 3.—Percent of Corn Plants Killed Prematurely by One or More Inoculations per Stalk With *Diplodia zeae* at Silking Time, Hybrid Ill. 1570, Urbana, 1957

Number of internodes inoculated	Internodes inoculated above the main brace roots	Percent prematurely dead plants 7 weeks after silking
None.....		19.4
1.....	second	31.9
2.....	first and fourth	43.4
3.....	first, third, and fifth	54.2
L.S.D. ^a at the 5-percent level.....		10.2

^a L.S.D. means least significant difference.

When several diseases are present, this method does not give specific information on susceptibility to any particular pathogen. This is sometimes true even though stalks have been inoculated, for the effects from natural infections are additive and may even be more severe than those from the inoculation.

Broken Stalks

Ratings for broken stalks sometimes correlated well with ratings for stalk rot (44, 72, 87). However, at other times (104, 111), no such relationship was found to exist. When a large number of hybrids were tested in Illinois, the hybrids in each test being to a considerable extent different, a significant correlation was found in 3 out of 4 tests between (a) plants killed prematurely in mid-September by stalk rot resulting from natural infection and (b) broken stalks at harvest time. In the fourth test, a low positive correlation was obtained. Some severely rotted hybrids stood better than the average in every test and vice versa, but these were exceptions. Stalk rot generally increases the susceptibility of the stalks to breaking (23), but other factors are also involved. Among these are heritable differences in the strength of stalks (36, 59) and differences among plants in response to variations in soil nutrients and in density of population (93). A difference in the number of plants may occur with different progenies, even though the same planting rate is used, because of differences in germinability of seed or because of differences in susceptibility to seedling blight. A third factor in the prevalence of broken stalks is the severity of wind storms, and a fourth is the amount of feeding by corn borers. Thus broken stalks are not always a good measure of stalk rot prevalence.

Stalk breaking caused by stalk rot ordinarily does not take place until the plants have died. In this respect it differs from breaking caused by corn borer injury. Plants severely affected by stalk rot usually die prematurely, and therefore it would seem better to determine the percentage of prematurely dead plants. However, if infection develops late in the season, little premature dying may take place, though stalk breaking still may occur after maturity. In some inbreds and hybrids, the tendency is for the stalks to break several feet from the ground even though the principal rot is lower. Durrell (23) found that in sound stalks the first node above ground has about twice as much breaking strength as the fourth node. This relationship probably varies with different inbreds and hybrids. The amount of softening within the rotted area, as well as softening from premature dying

above the rotted area, no doubt differs in different kinds of corn. How these factors vary presumably determines where the stalk breaks.

Broken stalks, of course, are a good character for the plant breeder to consider, regardless of whether they are the result of disease or of other conditions. Furthermore, corn plants that are able to stand even though the stalk has rotted certainly are more desirable than those that break. Sprague (88) observed that satisfactory measurements of differences between inbreds in the stalk-breaking tendencies which they transmit to crosses can be made only in hybrid combinations.

Firmness of Stalks

The amount of rot present is sometimes determined by pinching the stalks to test their firmness (68) rather than by noting how many have fallen. Since these methods are related to each other, they have the same merits and faults when used for diagnosis. Softening may be the more dependable symptom, however, since breakage not only depends on the force of the wind but also occurs when the stalk is weakened by whatever cause (see page 37). Testing for softness is frequently combined with visual observations of rot when making rot-prevalence determinations.

Surface Discoloration

Recording the prevalence of stalk rot on the basis of discoloration and of the presence of fruiting bodies has the advantage that it measures the rot directly. This method is suitable when the rot is due to natural infection but not for measuring the rot caused by artificial inoculation. The procedure has the disadvantage of being considerably slower than some other methods. The chief stalk rot pathogens in Illinois, *Diplodia zeae* and *Gibberella zeae*, cause a dark discoloration in the infected areas, particularly the areas killed while the plants are green (Figs. 1, 5, 6, 25, 27). These discolorations can be easily seen on the surface of the stalks after the lower leaf sheaths have been removed.

Measuring rot on the basis of discoloration required deciding how extensive the discoloration had to be for the stalk to be judged as rotted. After this standard was established, the plants were simply recorded as plus or minus for stalk rot and the percentage determined. Stalks possessing fruiting bodies of stalk rot pathogens were always classed as rotted. Severe infection with charcoal rot could usually be recognized by a close examination of the exterior of the stalks. As

the stalks were not cut, the process did not interfere with obtaining yield data. This method was especially useful when data for premature dying could not be used for various reasons, such as the occurrence of severe leaf blight or maturity.

Another method tried, based on discolorations (lesions), offers a more accurate numerical approach but requires more time and requires sacrificing the stalks before maturity. This method is useful, however, for certain purposes as it is precise and leaves little to personal judgment. Ten stalks from each of four replications were cut in late August to mid-September, depending on the season and the hybrid. Each stalk was cut so as to include the first four nodes above ground. The stalks were then laid on a table in order to have them convenient for accurate examination. Leaf sheaths and brace roots were removed, and a record was made of the number of infected nodes per stalk. Any node bearing a lesion having approximately the area of a circle $\frac{1}{4}$ inch or more in diameter was counted as infected. This was followed by plating to determine the cause of the infection.

There was an association between the number of infected nodes and the average size of lesions, and a highly significant correlation between the number of infected nodes and the aggregate size of the lesions. The data presented in Table 1, Columns G and H, give the average number of infected nodes per stalk as indicated by surface discolorations. By far the larger number of natural infections in 1957 was caused by *G. zeae*. Nodal infection by *G. zeae* (Column G) correlated significantly with the spread of rot from inoculation with *D. zeae* and with premature dying in all three categories (Columns D, E, F). The incidence of diseased nodes caused by natural infection with *D. zeae* correlated with the spread of rot and with premature dying from *D. zeae* inoculations.

The first two hybrids listed in Table 1 were also grown with ear shoots removed at or soon after pollinating time and with ears normal but the distal half of all leaves removed a few days after pollinating. The effect of these manipulations on stalk rot will be discussed later, but it should be stated here that ear removal greatly reduced nodal infections and leaf clipping increased them. These conditions correlated highly with premature dying of plants.

Internal Discoloration

Some investigators (32, 42) have split the stalks lengthwise from the ear to the soil level and then rated the stalks for the amount of internal discoloration or rot resulting from natural infection. Standards for rating are established at the outset. This would seem to be a

good direct approach, but this method, like the one involving surface discoloration, is better adapted to detailed studies than to routine evaluations because it is time consuming.

The data should be obtained before the leaves begin to die as a result of maturity. If considerable dying from stalk rot infection has already occurred at the time that the data are taken and if relatively healthy plants are still green, the dead stalks should not be split but simply be given the maximum score. Whether the rot development in dead stalks is faster or slower than in live stalks depends largely on the moisture content of the stalks.

A discussion of internal discoloration resulting from the use of artificial inoculation is given under "Area involved by rot," page 79.

DAMAGE CAUSED BY STALK ROTS

Broken stalks as a diagnostic symptom of stalk rot have already been discussed. They also may cause considerable loss to the crop (Fig. 19). Ears from broken stalks are difficult to harvest, and many are missed by the picker. Ears in contact with the ground may become moldy and rotten in moist weather. Lodged corn often clogs the picker, causing delay and trouble. Furthermore, when ears are plowed down,



Stalk breaking caused by natural infection primarily with *Diplodia zeae* in a commercial hybrid in a farmer's field. (Fig. 19)

a large number of the kernels germinate in the following spring and produce a volunteer stand of corn in another crop. Thus, the damage may be considerably greater than simply the grain lost on the ground.

A direct loss in yield also occurs. This has been determined in 15 hybrid corn tests in which more than average stalk rot damage occurred at the locations indicated in Table 4. The tests contained 50 to 81 entries each. The original data give the actual percentages of incidence of stalk rot for each hybrid (12, 13, 21, 71, 72, 73), based usually on premature death of plants. An indication of the range in differences between hybrids is given in Tables 2 and 5.

In every test, hybrids differed widely in susceptibility to stalk rot, even though they were commercial hybrids and the especially susceptible ones had been eliminated by seedsmen in their own testing programs.

Table 4.—Percentage of Plants Damaged by *Diplodia* and *Gibberella* Stalk Rot Correlated With Yield of the Current Crop and With Yield and Grain Moisture of the Same Hybrids Grown in the Same Area in Another Year When Stalk Rot Damage Was Below Average

Year	Location	Correlation coefficients for percentage of stalk rot incidence with:		
		Yield in the current crop	Data for the same hybrids when stalk rot was less damaging ^a	
			Yield	Grain moisture
		A	B	C
1938.....	Reddick	-.04	+.13	-.59**
	Paxton	+.13	+.19	-.25
	Sullivan	-.66**	+.33*	-.73**
	Albion	-.57**	+.36*	-.91**
1939.....	Cambridge	-.47**	-.15	-.02
	Littleton	-.75**	+.41*	-.08
	Sullivan	-.41**	+.17	-.22
1941.....	Mt. Pulaski	-.11	+.07	+.05
	Sullivan	-.05	+.59**	-.10
1950.....	Sheldon	-.40**	-.17	-.38*
1951.....	Galesburg	-.48**	+.06	-.59**
	Sheldon	-.61**	+.12	-.15
	Sullivan	-.42**	-.09	-.40*
1953.....	Galesburg	-.24*	+.13	-.13
	Ridgway	-.43**	+.42**	-.23

^a Stalk rot in year indicated at left correlated with yield and grain moisture at harvest for the same hybrids tested at the same location 1 or 2 years earlier or later when stalk rot was less damaging and all plants matured more nearly normally.

* Significant at the 5-percent level.

** Significant at the 1-percent level.

Table 5.—Average Yield of the 10 Hybrids With the Least Stalk Rot and Average Yield of the 10 Hybrids With the Most Stalk Rot at Several Locations in Two Years

Year	Location	Number hybrids in test	Average of 10 hybrids with least stalk rot		Average of 10 hybrids with most stalk rot		Reduction in acre yield
			Stalk rot	Acre yield	Stalk rot	Acre yield	
			<i>perct.</i>	<i>bu.</i>	<i>perct.</i>	<i>bu.</i>	<i>bu.</i>
1951.....	Galesburg	81	4.2	111	28.0	101	10
	Sheldon	81	6.3	112	35.4	98	14
	Sullivan	81	2.9	104	34.1	96	8
1953.....	Galesburg	81	2.0	95	25.2	89	6
	Ridgway	60	5.7	102	24.6	88	14
Average reduction, all areas		..	...	...		..	10

It is well known that there are many factors that determine yield. If the same hybrids could have been grown with and without stalk rot in the same tests, the actual bushel loss from disease could have been determined. Such a test was not possible. However, the large number of entries in the tests reported in Table 4 minimized the effect of the factors other than stalk rot. The data show that 10 of the tests had highly significant negative correlations between the incidence of stalk rot in the various hybrids and the yield obtained from the same plants. As the stalk rot percentage went up, the yield went down. There was only one small positive correlation, and it was nonsignificant (Table 4, Column A).

Furthermore, there is some association between stalk rot susceptibility and the ability to produce a high yield (see page 52). Thus, the correlations in Table 4, Column A are even more meaningful, and the bushel losses in yield given in the following paragraph actually may be higher than indicated.

Yield losses are impossible to estimate with accuracy. To obtain some numerical idea of the differences in yield caused by stalk rot, acre yields were averaged for the 10 hybrids with lowest stalk rot rating and the 10 with highest rating in each of 5 tests for which the most recent data were available (72, 73). The average difference in yield between the two groups was 10 bushels (Table 5). Although this is a direct measure in bushels, these data have no direct bearing on average losses from stalk rot. On the one hand, stalk rot prevalence was above average in these tests although these fields were by no means among the worst seen, and, on the other hand, even those with lowest

stalk rot prevalence had an average of 4 percent badly diseased stalks and, of course, many more that were diseased to a lesser extent. Furthermore, as these experimental tests were hand picked, the yields obtained do not take into account the usual loss on farms due to difficulty of harvesting when corn is lodged. Considering all these aspects, an estimate of an average annual loss of 7 to 10 percent appears to be valid.

A determination of yield losses from cornstalk rots in Illinois in 1958 has been reported by Hooker and Britton (34). When the corn was mature, 10 comparisons were made in each of 17 fields, between plants with (a) green stalks, (b) stalks rotted and dead but standing, and (c) stalks rotted, dead, and lodged. Plants of the three classes were selected in close proximity to each other and in such a manner as to eliminate differences caused by plant competition. The ears were dried to uniform moisture content, shelled, and weighed. If the plants with green stalks are considered as healthy, the loss was 18 percent for plants having stalk rot but standing and 27 percent for plants rotted and lodged. Fifty-eight percent of all the plants in the fields studied had stalk rot to the extent of (b) or (c) above, and the general loss from stalk rot in these fields was calculated as 10 percent.

DeVay *et al.* (19) estimated the average annual loss from stalk rots in Minnesota as 10 percent.

Michaelson and Christensen (67), measuring the results of stalk inoculations in two hybrids over a 3-year period, found an average decrease in yield of 9.7 percent when *Diplodia zeae* was used and a 6.8 percent decrease with *Gibberella zeae*. Troyer (97), working with five hybrids, found that plants inoculated with *D. zeae* in only 1 internode suffered an average yield reduction of 2.3 percent and that when 3 different internodes were inoculated with this fungus, the reduction was 5.4 percent. Although small, these yield reductions were highly significant. One difficulty with yield-loss determinations from artificially inoculated plants is that both the check and the inoculated plants are subject to damage from natural infection.

FACTORS INFLUENCING NATURAL ROT DEVELOPMENT

Seed Infection

Whether *Diplodia* infected seed is of significance in initiating *Diplodia* stalk rot is a disputed point. Durrell (22) and Clayton (11) concluded that *Diplodia zeae* does not spread into the stalks from infected seed. McNew (61), however, demonstrated experimentally that the use of infected seed may later result in crown infection. In three

years of field experiments made in Illinois with *Diplodia* infected seed (53), the incidence of stalk rot, as judged by stalk breaking, was very little if any higher than the incidence of stalk rot in plants grown from seed nearly free of disease. For this experiment, seed was selected that had a high percentage of infection as well as good germinability (Fig. 28 in literature reference 54). The percent of seed corn infected with *Diplodia* has been very small in recent years (48, 100).

Less is known about the possibility of stalk rot originating from seed infection with *Gibberella zeae*. Although this fungus is very important as a cause of stalk rot, ordinarily it causes less seed infection in Illinois than *D. zeae*, and so in any case seed infection would usually be a negligible cause of stalk rot. *Fusarium moniliforme* also causes seed infection as well as stalk rot, but it is doubtful that there is any important connection between the two. This fungus seems to be so ubiquitous in cornfields that inoculum is adequate with or without planting infected seed.

Weather Conditions

It has been clearly demonstrated that hot, comparatively dry weather favors the development of charcoal rot (58, 109) and that hot, damp weather favors bacterial and *Pythium* stalk rot. With regard to our most damaging stalk rots, *Diplodia* rot may be rampant in some years and *Gibberella* rot in others, or both may be heavy or light in the same year (51, 52). Conditions, of course, are not uniform throughout the state, nor is ear rot always increased by the same conditions that increase stalk rot. In 1951, stalk rot damage was above average at Galesburg, Sheldon, and Sullivan (72), but light at Brownstown. Ear rot prevalence caused by *Diplodia zeae* also ranked similarly at these locations (72). In 1950, on the other hand, of the various locations where tests were made, stalk rot was most prevalent at Sheldon, while ear rots caused by *D. zeae* and *G. zeae* were considerably higher at Galesburg and Sullivan (71).

Durrell (22) concluded that the amount of rainfall in August determines the amount of dry rot (*Diplodia*) but he did not distinguish between ear and stalk rot. Koch and Murwin (45) state that abundant rainfall during the latter part of the growing season appears to increase the amount of *Diplodia* stalk rot. Ullstrup (100) observed that the severity of *Diplodia* stalk rot is increased by wet weather in August and September, especially when preceded by unusually dry weather in June and July. According to these reports, moisture conditions favorable for *Diplodia* stalk rot are about the same as those favorable for *Diplodia* ear rot (50).

Michaelson (66) kept the soil of part of a corn test saturated with water from two weeks before inoculating until three weeks after inoculating. The unsaturated area had adequate rainfall for good corn growth. The greatest spread of rot from *D. zeae* and *G. zeae* stalk inoculations occurred in the unsaturated area.

Temperature also has an influence on *Diplodia* and *Gibberella* stalk rot development. Michaelson (66) observed that stalk rot appeared to be least severe at St. Paul, Minnesota, in comparatively cool summers. In an experiment in which inoculated corn was grown under controlled temperatures of 65° and 85° F., *D. zeae* and *G. zeae* both caused more stalk rot at the higher temperature.

Other observations indicate that the optimum temperature for damage by *Diplodia* is a little higher than that for *Gibberella*.

The differences in yearly variation are more noticeable for the rots that cause premature dying and stalk breaking than for the rots that are not evident until the corn is mature. Yearly variations occur not only in damage resulting from natural infection but to some extent also in that resulting from artificial stalk inoculations (66, 111).

Weather conditions might be expected to influence stalk rot prevalence in at least three ways: (a) abundance of spores produced and carried to corn plants, (b) conditions favorable for the spores to be washed behind the leaf sheaths and to germinate, and (c) susceptibility of the host to infection or to damage after infection.

Inherited Resistance

That differences in resistance or susceptibility to *Diplodia* and *Gibberella* stalk rot exist in inbreds and hybrids is so well established that it need not be discussed here. In the 1938 *Diplodia* stalk rot epidemic in Illinois, hybrids containing inbred R4 were so badly injured that the use of R4 was discontinued soon thereafter. Previous to 1938, however, in relation to some other inbreds, R4 had been considered to be comparatively resistant (16, 17, 40). No corn plants are immune and resistance is a comparative quality. Of inbreds now in wide use in the corn belt, B14 and C103 possess comparatively good resistance to *Diplodia* and *Gibberella* stalk rot.

Mode of inheritance. The mode of inheriting resistance to stalk rot has been observed principally for resistance to *Diplodia zeae* and *Gibberella zeae*, especially the former. Jugenheimer (42), Sprague (88), and Hooker (32) have reported that resistance appears to be inherited in a typically quantitative pattern and that hybrids are resistant usually in proportion to the number of resistant inbreds used

in their synthesis. Jugenheimer (42) concluded that resistance to *Diplodia* stalk rot is partially dominant. Zuber *et al.* (111), working with 6 inbreds, found that the agreement in stalk rot ratings between parents, F_1 and F_2 progenies, and backcrosses was fair for both *D. zeae* and *G. zeae*. Thus, it appears that tests of inbreds will, in general, yield as much useful information as tests of crosses. Data by Hooker and Russell on stalk rot reaction of B14, resistant, and Oh41, susceptible, and the F_1 and F_2 crosses and backcrosses were presented by Sprague (88). After artificial inoculation with *D. zeae*, the resistance of the F_1 was intermediate between that of the two parents but a little nearer to that of the resistant parent. The F_2 showed a little less resistance than the F_1 , while the two backcrosses tended to approach the reaction of their respective parents.

Data on the inheritance of resistance to stalk rot are still meager. As yet there appears to be no report on the observance of any specific combining value contributed by parents to their progenies, but observations at Urbana indicate that this effect does exist. In addition, some inbreds appear to be more potent in transmitting resistance than others (42).



Broken stalks in inbred Ky27 caused by natural infection with *Gibberella zeae* in a test plot surrounded by more resistant inbreds. (Fig. 20)

Association between resistance to *Diplodia* and to *Gibberella* stalk rots. Severe outbreaks of *Gibberella* stalk rot have rarely been associated with low incidence of *Diplodia* rot in inbreds or hybrids grown in test plots. An exception occurred in 1946 at Urbana and at Bluffs (51). That the epidemic was not caused by *D. zeae* became evident in early September, before the causal fungus fruited, because the inbreds L317, Kys, K4, and Ky27 (Fig. 20), and some crosses involving them, died and broke over early. These inbreds were known to have some resistance to damage from natural infections by *D. zeae*. Laboratory tests proved the rot to be caused by *G. zeae*. This is an example where susceptibility to the two fungi was not associated.

Data were obtained in 1957 on the extent of natural infection by these two fungi in nine single crosses (Table 1, Columns G, H). The correlation for *Diplodia* and *Gibberella* rot in these hybrids was highly significant, but by an analysis of variance a significant interaction was shown between the two. This means that while there is a strong tendency for the susceptibility to stalk rot caused by these two fungi to be similar, occasional inbreds may react in an opposite manner to these pathogens.

Other reports on this subject are based on the results from artificial inoculations. Semeniuk (80) reported a highly significant correlation among inbreds with respect to the extent of rot caused by each of these fungi, but a nonsignificant correlation among hybrids. DeVay *et al.* (18) published data on the susceptibility of 110 kinds of corn to *Diplodia* and *Gibberella* stalk rot resulting from artificial inoculation. There apparently was no correlation in reaction of the two fungi. Considering only the entries rated as resistant or susceptible to these two pathogens, 7 entries rated either resistant or susceptible to both pathogens and 5 rated resistant to one and susceptible to the other. On the other hand, Hooker (32), Sprague (88), and Zuber *et al.* (111) reported correlations between amounts of rot obtained from stalk inoculations with the two fungi to be significant at either the 1-percent or the 5-percent level.

In inoculation tests made at Urbana in 1952, two single crosses did not react the same to *D. zeae* and *G. zeae*. WF9 x Hy2 had significantly more rot and prematurely dead plants when inoculated with *D. zeae* than with *G. zeae*. On the other hand, in Ky27 x 33-16, *D. zeae* produced less and *G. zeae* more rot than they had in WF9 x Hy2, indicating a reversal in relative susceptibility (Table 6, Fig. 21). This is in agreement with the high susceptibility of Ky27 to natural infections with *G. zeae* (Fig. 20). In an inoculation test involving nine single crosses in 1957 (Table 1, Columns B, C) the correlation for internodes

Table 6. — The Effect of Leaf Clipping on the Development of Stalk Rot, Prematurely Dead Plants, Broken Stalks, and Yield of Grain in Two Hybrids (Some of the Plants Artificially Inoculated With *Diplodia zeae* and *Gibberella zeae* by the Toothpick Method About Two Weeks After Silking and the Leaves Clipped the Day of Inoculation) Urbana, 1952

Hybrid	Fungus used for inoculation	Average number of internodes rotted per stalk ^a		Prematurely dead plants ^a		Stalks broken below the ear ^b		Acre yield ^b	
		Leaves normal	Leaves clipped	Leaves normal	Leaves clipped	Leaves normal	Leaves clipped	Leaves normal	Leaves clipped
Ky27 x Ind. 33-16	Diplodia	1.62	1.61	16	32**	8	13*	98	83**
	Gibberella	1.08	1.03	13	28**	9	13	105	86**
	check ^d	.19	.21	6	19**	7	11	109	96**
Ind. WF9 x Ill. Hy2	Diplodia	2.02	2.06	28	48**	22	30**	96	81**
	Gibberella	.76	.80	4	17**	18	21	99	89**
	check ^d	.33	.31	0	9**	2	9**	99	91**
L.S.D. at the 5-percent level		.32	.32	7	7	5	5	6	6
Both hybrids	Diplodia	1.82	1.84	22	40**	15	22**	97	82**
	Gibberella	.92	.92	9	23**	14	17*	102	88**
	check ^d	.26	.26	3	14**	5	10**	104	94**
L.S.D. at the 5-percent level		.23	.23	5	5	3	3	4	4

^a Determined September 15. See also Fig. 21.

^b Determined November 3.

^c Percentages converted to angles (arc sin transformations) in order to obtain a more accurate statistical interpretation.

^d Sterile toothpicks were inserted into the stalks in the same manner as with the fungus inoculations.

* Indicates significance at the 5-percent level between the results from plants with normal and those with clipped leaves.

** Indicates significance at the 1-percent level between the results from plants with normal and those with clipped leaves.

rotted by *D. zeae* and *G. zeae* was significant at the 5-percent level, but the interaction for amount of rot between the nine inbreds was highly significant, indicating lack of uniform association for resistance to these two fungi.

Nature of resistance. Holbert *et al.* (31) conducted experiments involving prevention of pollination on the one hand and partial defoliation on the other and concluded that a low carbohydrate content of the stalks increased susceptibility to *Diplodia* stalk rot. Sayre *et al.* (79) had determined earlier that the prevention of fruiting increases the sugar content of stalks and that leaf clipping reduces it. They found also that the increased sugar was primarily sucrose and not free reducing sugars. DeTurk *et al.* (16, 17) made chemical analyses of the stalks of a susceptible and of a more resistant single cross during the first half of September. They found that the susceptible hybrid had less total sugars in the stalks and in the shanks than did the more resistant single cross. Differences were greater or at least as great in the lower part of the stalk as higher up. Cutting off about 30 percent of the leaf area 10 days after pollination increased susceptibility to



Ky27 x 33-16

WF9 x Hy2

Cornstalks of two single crosses split open 33 days after inoculating. A, inoculated with *Diplodia zeae*, and B, with *Gibberella zeae*. C, checks in which sterile toothpicks had been inserted in the same manner as for the inoculations. (Fig. 21)

Diplodia rot. It also reduced the sucrose content of both hybrids considerably, but caused practically no difference in the amount of the reducing sugars present. It was surmised that resistance might be associated with the nitrogen-sucrose ratio. This theory is strengthened by the results reported by Zuber *et al.* (111). They found a highly significant positive correlation between susceptibility to *Diplodia zeae* and *Gibberella zeae* and to nitrogen content. They found also that rot ratings for both pathogens were highly correlated negatively with cellulose content. There were negative correlations also for ash, crude fiber, and lignin. In France (65), a low sugar content of cornstalks was found to be associated with increased susceptibility to anthracnose stalk rot caused by *Colletotrichum graminicolum* (Ces.) Wils. According to other investigators (35), a low sugar content of the host increases susceptibility to some diseases and decreases it to others.

Hoadley (30) as a result of anatomical studies of infected stalks concluded that mechanical barriers were not responsible for resistance to *D. zeae*.

Johann and Dickson (40) reported an inhibiting substance found in cornstalks and extractible by ether. They used 11 inbred lines and 5 single crosses that varied in their susceptibility to Diplodia stalk rot. Up to shortly after pollinating time, extracts from all inbreds and hybrids retarded the growth of *D. zeae*, *G. zeae*, and *Nigrospora oryzae* in culture. As the ears developed, some lines soon lost the growth-retarding effect while some others retained it to a considerable extent. This difference coincided with the difference in susceptibility to stalk rot. Juice pressed from stalks gave similar results. The nature of the retarding substance was not determined.

On the other hand, removal of ears or partial defoliation of plants, while greatly affecting the susceptibility of plants to natural development of Diplodia and Gibberella rot, did not change the efficacy of the growth-inhibiting character of the sap extractions. This indicates that there are further unknown aspects of the nature of stalk rot resistance.

Years after Johann and Dickson reported their results, Barnes (4) obtained results that substantiated those discussed above. He used tissues of roots and stalks from which extracts were made by various methods. At silking time, extracts, particularly ether extracts, from both resistant and susceptible inbreds and hybrids contained a substance fungistatic to *G. zeae*. Further tests were made at two-week intervals during the ensuing two months. The extracts, which were made at successive intervals from both susceptible and resistant plants, gradually lost the inhibiting substance, but the rate of loss was greater in the extracts from susceptible plants.

Taylor (94) worked to a limited extent with juice pressed from resistant and susceptible cornstalks. He obtained results that tended to be the opposite of those obtained by Johann and Dickson. Juice from resistant stalks supported the growth of *D. zeae* somewhat better than did the juice from susceptible stalks.

Pappelis (69) concluded from his experiments that no correlation existed between the soluble carbohydrate content of cornstalks and susceptibility to *Diplodia* stalk rot. He observed that in susceptible stalks the pith tended to have a whitish appearance caused by air vacuoles in the cells. The difference could be measured between the water content of the internode pith of susceptible and of resistant stalks. The cells containing air were low in specific gravity and were found to be nonliving and hence susceptible.

Craig (14) investigated the relation between the specific gravity of pith tissue and the development of stalk rot resulting from inoculation with *Diplodia zeae* and obtained results that in this respect support the findings of Pappelis. He used 12 inbreds ranging from resistant (Ia. B14, Ill. R101, and Conn. C103) to very susceptible (Ill. R53, R80, and R168). Internodal pith cores were taken from non-inoculated healthy plants at silking time and at intervals during the next four weeks. There was a tendency for specific gravity to diminish with time after pollinating, but at all dates on which samples were taken there was a highly significant inverse correlation between specific gravity and rating for susceptibility. Healthy plants of resistant and susceptible lines were used to assure that the differences in specific gravity were associated with susceptibility and were not the result of rot incidence. Craig also found that during the first four weeks after pollinating, the total sugar content of rot susceptible stalks decreased progressively while that of resistant stalks increased.

Thus, much still remains to be learned about the nature of resistance to the stalk rot diseases and about the characteristics or conditions associated with resistance.

Earliness

The use of early-maturing varieties or of very early planting which results in early maturity has been mentioned at various times as contributing to stalk rot susceptibility (6, 45, 71, 100, 105). Data obtained from 15 tests in Illinois (12, 13, 21, 71, 72, 73) lend further support to this conclusion (Table 4). These stalk rot data were obtained in years when stalk rot prevalence was above average. Grain moisture, which is used as a measure of maturity at harvest, was determined in

years when there was less than average stalk rot and thus ears did not dry prematurely. There was a negative correlation between severity of stalk rot and normal grain moisture. Thus the later the corn, the less the stalk rot. However, there were no extremes in maturity, for all the hybrids selected for each test were considered to be well adapted to the location where grown. In only one instance was the correlation reversed and that figure was extremely low. Four of the negative correlations were highly significant and two were significant at the 5-percent level.

An early variety appears to be at a disadvantage compared with a later one because it reaches the stage of susceptibility sooner. The rot has a longer time in which to act, and warm weather promotes a more rapid growth of the fungus. It has been observed that a full-season variety becomes more susceptible when grown a considerable distance south of its area of adaption, for it behaves as an early variety. For instance, Young *et al.* (108) observed that when the same single crosses were planted in Minnesota, Missouri, and Oklahoma and were inoculated with *Diplodia maydis* (Berk.) Sacc. (synonym for *D. zeae*), there was less stalk rot in Minnesota than in the states farther south.

Earliness is only one character influencing susceptibility. Other factors may counteract it so that certain early hybrids may be comparatively resistant.

Yield

Susceptibility to *Diplodia* and *Gibberella* stalk rot is influenced by grain yield. When a natural stalk rot epidemic is in progress in a hybrid, the first stalks to die from disease are ones bearing two ears. The next to die are stalks bearing one ear. Stalks that bear no grain or almost none remain green until harvest time. Holbert *et al.* (31), Hoadley (30), and Michaelson (66) reported less *Diplodia* or *Gibberella* rot resulting from artificial stalk inoculations when plants were not allowed to bear grain. On the other hand, Pappelis (69) found that removal of ear shoots at pollinating time had little effect on rot due to inoculation with *D. zeae*, and Jugenheimer (42) reported increased spread of rot from inoculation with *D. zeae* when plants were earless because pollination had been prevented. In Illinois, hybrids that were defruited shortly after pollination were found to be comparatively free from natural stalk infections with *D. zeae* and *G. zeae*.

Correlations were determined between (a) stalk rot percentage ratings of hybrids when stalk rot damage was high and (b) yield of grain of the same hybrids when stalk rot percentages were low. The

results of 15 such comparisons are given in Table 4, Column B. All but 3 of the correlations were positive, 2 of them highly significant, and 3 others significant. None of the negative correlations was significant. Thus there is strong evidence that susceptibility is associated to a considerable extent with potential high yield. This relationship is to be expected in view of the relationship between the sugar content of stalks and rot susceptibility (see pages 48 to 51). As the susceptible plants had a progressively lower sugar content with time after pollination (14), they appear to be more active in translocating sugars from the stalks to the ears. Since the principal emphasis in corn breeding and reporting of results has been on yield and since a conflict exists between high yield and stalk rot resistance, it is not surprising that most hybrids behave badly during a stalk rot epidemic. No doubt a high degree of resistance can be combined with high yielding ability, but if this is to be done, most plant breeders will have to give more attention to disease resistance than they have up to now.

Leaf Damage

The observation that leaf blight or partial defoliation may increase Diplodia stalk rot damage apparently was reported first by Holbert *et al.* (31). It was determined at Urbana (47) that partial defoliation also increased the damage from Gibberella stalk rot. In a test of 81 commercial hybrids at Sullivan, Illinois (72), in 1951, a correlation of 0.788 was found between ratings on September 14 for loss of leaf area from northern leaf blight and ratings on September 27 for stalk rot severity based on stalk discolorations. Michaelson (66) reported that cutting the leaves off half way back from the tip two weeks before inoculation, was somewhat effective in increasing rot resulting from inoculations with *D. zeae* or *G. zeae*, while cutting them the day of inoculation had little or no effect. Breaking the leaves was less effective.

As hail damage and grasshoppers and other insects may cause serious degrees of defoliation, this type of mechanical damage may also be expected to increase stalk rots if it occurs during the critical period from two weeks before tasseling until the kernels dent.

When inoculations were made with *D. zeae* and *G. zeae* two weeks after silking, the spread of rot was not influenced by cutting off about half the leaf surface on the day of inoculation (Table 6). This agrees with the results obtained by Hoadley (30), Jugenheimer (42), and Michaelson (66). However, three other very important effects resulted from leaf clipping. First, natural infection from *D. zeae*, *G. zeae*, and *Fusarium moniliforme* increased markedly. As shown at the bottom

Table 7. — Fungi Isolated From Rot-Discolored Areas of Cornstalks in Relation to Artificial Stalk Inoculation and Leaf Clipping, Hybrid U. S. 13, Urbana, 1952

Inoculum	Method of inoculating	Tissue from which isolations were made	Leaf condition	Stalks tested	Fungi isolated				
					<i>Diplodia zeae</i>	<i>Gibberella zeae</i>	<i>Fusarium moniliforme</i>	<i>Cephalosporium acremonium</i>	Others
				number	perct.	perct.	perct.	perct.	perct.
<i>Diplodia zeae</i>	Toothpicks	Interior of stalk	Normal	24	95.8	0	8.3	0	0
<i>Diplodia zeae</i>	Toothpicks	Interior of stalk	Clipped	24	95.8	0	12.5	0	0
<i>Gibberella zeae</i>	Toothpicks	Interior of stalk	Normal	64	0	78.1	20.3	3.1	1.6
<i>Gibberella zeae</i>	Toothpicks	Interior of stalk	Clipped	64	0	81.3	18.8	3.1	1.6
None	Sterile toothpicks	Interior of stalk	Normal	64	0	1.6	57.8	46.9	10.9
None	Sterile toothpicks	Interior of stalk	Clipped	64	0	6.3	59.4	48.4	15.6
None	None	Cortex ^a	Normal	52	1.9	15.4	1.9	0	0
None	None	Cortex ^a	Clipped	52	11.5	69.2	15.4	0	11.5

^a Natural infection originating at nodes.

of Table 7, when the leaves were clipped, the incidence of lesions on the cortex increased 4 to 8 times compared with the normal incidence. These data were obtained from 18-inch sections taken from uninoculated plants. The lower ends of these sections were cut just above the ground. They were cleaned and brought to the laboratory about four weeks after the leaves had been clipped. A piece was agar plated from the largest lesion on each stalk that had become naturally infected.

The second outstanding effect was in prematurely dead plants (Table 6). Premature dying increased very significantly when plants had been inoculated with *D. zeae* or *G. zeae* and the leaves clipped. Premature dying was also increased in the clipped checks but to a lesser degree. This effect was no doubt caused by the increase in natural infection.

The third significant effect of leaf damage was an increase in broken stalks (Table 6). This response is often closely related to premature dying. Furthermore, leaf clipping and inoculation had a pronounced effect on yield. When the leaves were normal, only inoculations with *D. zeae* reduced the yield of Ky27 x Ind. 33-16, but when the leaves had been clipped, *G. zeae* as well as *D. zeae* significantly lowered the yield of this hybrid. *D. zeae* also decreased the yield of WF9 x Hy2 when leaves had been clipped.

The general effect appears to be as follows: (a) inoculations with *D. zeae* or *G. zeae* affected plants with normal and clipped leaves about equally with respect to spread of rot, (b) damage from natural infection was more pronounced in plants with clipped leaves than in plants whose leaves were left normal, and (c) in inoculated plants with clipped leaves there was an additive effect resulting from inoculation and increased natural infection.

Jugenheimer (42) also found that, in general, plants with clipped leaves died earlier than normal plants, but in some other respects his results do not agree with those given above. When the rot examined by Jugenheimer was judged on the basis of split open stalks, the rot resulting from natural infection was about the same in stalks from the two classes of plants, but the rot resulting from inoculation, in some tests, was less when the leaves had been clipped. These differences in results have not been explained, but could possibly have been due to differences in environment.

European Corn Borer

A study was made from August 9 to September 20 in 1955 and 1956 of stalks infested with the European corn borer. Stalks were discarded if the rot in the areas where corn borers had fed was

Table 8. — Comparative Prevalence of Fungi Isolated From Lesions Resulting From Natural Infection on Green Cornstalks of a Total of Five Hybrids, August 9 to September 20. Urbana, 1955-1956

Class (position of lesion or rot)	Number of stalks per class ^a	Number of stalks from which the following fungi were isolated ^b										
		<i>Diplodia zeae</i>	<i>Gibberella zeae</i>	<i>Fusarium monili- forme</i>	Other Fusarium species	<i>Cephalo- sporium acromonium</i>	<i>Pyrenochaeta chlamy- dosporealis</i>	<i>Phaeo- sporia vaasii</i>	<i>Helmintho- sporium</i>	<i>Chaetomium</i> species	Alternaria species	Other fungi
Below soil level, apparently following an insect attack	261	4	10	182	14	14	46	4	2	14	15	21
Below soil level on an internode, no insect attack	562	7	15	224	0	45	202	4	0	7	7	52
Below soil level, at origin of a discolored root	59	3	0	34	2	10	16	4	0	2	4	3
At soil surface at origin of a root	110	11	13	47	1	3	17	20	3	8	3	8
At origin of a brace root ^d	181	16	46	81	9	7	10	5	3	9	7	15
At origin of a leaf sheath, above brace roots	265	53	151	72	2	8	4	2	6	0	12	14
At a rotted shoot bud	13	2	3	6	0	0	0	0	0	1	1	0
On an internode, independent of a node ^e	66	3	8	19	3	6	4 ^f	0	1	1	2	3
In interior of stalks following European corn borer attack	264	0	7	165	2	110	0	0	0	0	2	13

^a A stalk with several lesions of the same class was counted only once, but several classes were frequently found and recorded for the same stalk. These numbers are not accurate for comparative purposes because on August 9 lesions were primarily below ground only, while by September 20 many stalks with aboveground lesions had to be discarded because the rots had progressed so far that the place where infection had originated could not be determined definitely.

^b Some stalks yielded several fungi, thus the same stalk may be recorded in several columns.

^c Among these were *Mucorales*, *Penicillium* species, *Trichoderma* species, *Sclerotium botatolu*, *Pythium* species, and unidentified fungi.

^d Or at the origin of a leaf sheath at a node bearing brace roots.

^e Some of these discolored areas plated sterile.

^f Found only when lesions were within 8 inches of the soil.

continuous with or adjacent to rot at a node, since in that case the rot might have spread from the node rather than entered the stalk through the corn borer holes. Of the 264 stalks in which the rot must have entered through the corn borer holes, by far the largest number were infected with *Fusarium moniliforme* (Table 8). *Cephalosporium acremonium* was next in frequency. The "other fungi" class in Table 8 included principally *Mucor*, *Penicillium*, and *Trichoderma* species. Seven of the areas invaded by the corn borers contained *Gibberella zeae*, apparently as a result of the corn borer activity. No *Diplodia zeae* infections were found. This is in agreement with observations made on fungi gaining entrance through growth cracks (Fig. 7) and into corn ears (50) that infections with *D. zeae* are not significantly increased by mechanical injuries. This also seems to apply to a considerable extent to infections with *G. zeae*.

In an earlier work, during a year when there was an epidemic of *Diplodia* stalk rot (70), the writer reported that much *Diplodia* infection had entered directly through holes made by corn borers or had been carried into the stalk by larvae. As a result of further study, this assumption appears to have been incorrect. Infection with *D. zeae* and *G. zeae* usually starts at the nodes, that is, at the bases of the leaf sheaths, but as the fungus reaches the tunnels made by corn borers, it probably spreads faster than it would through sound tissue. Fig. 22-right, shows nodal infections with *D. zeae* above a hole made by a corn borer and a *G. zeae* lesion at the node below.

Fusarium moniliforme was the principal cause of the stalk rot damage associated with corn borer attack (Fig. 22-right), and at times the damage it caused was considerable. Christensen and Schneider (10) in Minnesota also reported that *Fusarium* was the most common species in rotted areas around corn borer tunnels. They found *G. zeae* and *D. zeae* in much smaller numbers, but in higher percentages than have been found in Illinois (Table 8). The method of taking data may not have been comparable, for they did not state whether these infections were necessarily the result of corn borer activity or whether some of them might not have originated at an adjoining node and then invaded the corn borer tunnels. They obtained a small number of *D. zeae* and *G. zeae* isolates from living and dead corn borer larvae, but here again *F. moniliforme* was the principal fungus found.

Taylor (95) in Iowa also reported *Fusarium moniliforme* and *Cephalosporium acremonium* as the fungi most commonly isolated from stalk rot in conjunction with corn borer tunnels. *Gibberella zeae* was isolated occasionally and *Diplodia zeae* rarely. Thus the results



Left, a shallow, brown, streaked discoloration which sometimes yielded *Fusarium moniliforme* when plated but more often was sterile. The streaks appeared to be directly beneath veins in the leaf sheath covering the internode. Center, large blotch independent of a node, at least a foot from the ground, an unusual occurrence, caused in this case by *Diplodia zeae*. Right, the dark, streaked discoloration originating at the corn borer hole was caused by *Fusarium moniliforme*. The nodal lesions at the top of the stalk at the right were caused by *D. zeae* and the large one at the bottom by *Gibberella zeae*. (Fig. 22)

from three different locations and from different years agree very well. Numerous bacterial isolations also were obtained in all these investigations. Taylor (95) made stalk inoculations with some of these bacteria, but obtained no more rot than occurred in the checks treated with sterile toothpicks. Michaelson (66) determined that wounds made with an instrument to simulate mechanical damage by corn borers did not change the susceptibility of the stalks above or below the wounded area.

Soil Fertility

It was reported in 1930 (54) that *Diplodia* stalk rot may be more prevalent when the plants are grown on soil having a high level of productivity than on less fertile soil. Observations supporting this statement have been made on the Morrow Plots, Urbana, where corn growing at several levels of fertility could be compared, and on farms where heavy fertilizer applications had been made. This relationship has also been observed by others (27), but it has occurred only on some farms and in some years and is not universal. It is a common experience among investigators to note that stalk rot is aggravated when potassium is low in relation to other plant food materials (46), but it is also true that in many cases severe rot damage has occurred even though the potassium supply was abundant. Stalk rot was outstandingly severe on the Morrow plots having high fertility, including high potassium, in 1949, 1955, 1957, and 1958. It was much less severe on adjacent plots of lower fertility.

Table 9 shows the effect on stalk rot of several kinds of fertilizer

Table 9.—Effect of Fertilizer Applications on Corn Yields and Stalk Rot Development Caused by *Gibberella zeae* and *Diplodia zeae* on the Agronomy Soil Experiment Field, Clayton, Illinois

Fertilizer application equivalents ^a			Acre yield 8-year average 1949-1956	Acre yield 1951	Rot damaged stalks 1951
N	P ₂ O ₅	K ₂ O			
lb.	lb.	lb.	bu.	bu.	perct.
0	0	0	80	80	16
80	0	0	84	84	40
80	80	0	83	76	49
80	80	80	100	110	17
0	80	0	80	84	21
0	80	80	90	85	13
0	0	80	93	88	17
120	120	120	101	102	16

^a For 80 pound equivalents: 400 pounds 20 percent ammonium sulfate, 400 pounds 20 percent superphosphate, and 133 pounds 60 percent muriate of potash. These were applied in the spring before plowing for corn, in a 4-year rotation. All the soil had been limed.



Left, stalk breaking resulting from stalk rot in hybrid U.S. 13 at Clayton, Illinois, soil experiment field when fertilizers added in pounds per acre for N, P_2O_5 , and K_2O had been 80, 80, 0. Right, a plot in the same experiment where fertilizer applications had been 80, 80, 80 (see Table 9). (Fig. 23)

applications on soil deficient in potassium. The experiments reported here were made on the Clayton experiment field in 1951, when stalk rot, resulting from natural infection, was above average in severity and was caused about equally by *Diplodia zeae* and by *Gibberella zeae* (52). The plot was shown to be deficient in potassium by the increases in yield which followed the application of potassium chloride. A deficiency in potassium when the nitrogen content of the soil was left unaltered did not aggravate stalk rot, for the rot was about as prevalent when potassium was added as when it was deficient. Nor was a deficiency of potassium in conjunction with a high level of phosphorus significant, since an addition of superphosphate alone had no effect on yield and little, if any, on stalk rot. When nitrogen fertilizer was added, either alone or with phosphorus, the prevalence of stalk rot greatly increased. But when all three fertilizer materials were used, even in large amounts, stalk rot percentages were no higher than in the untreated check. Differences in stalk breaking were fully as great as differences in stalk rot prevalence (Fig. 23). Similar results on the relation of the nitrogen-potassium chloride ratio to stalk rot have been reported by others (27, 68). Otto and Everett (68) found that not all hybrids responded to variations in fertilizer treatment to the same extent with respect to stalk rot prevalence.

Younts and Musgrave (110) found that increasing the rate of

potassium chloride fertilizer applied to corn decreased stalk rot incidence, but this was not the case when potassium sulfate or potassium metaphosphate was used. Also, a close correlation existed between the percentage of plants having stalk rot and the percentage of chloride in the ear leaf. Thus it appears, on some soils at least, that the effect on stalk rot control of applying muriate of potash is not from the potassium but from the chlorine in the compound.

Experiments on the effect of nitrogen on cornstalk rot were conducted at Urbana for two years on a soil having good basic fertility. The available potassium content was 250 to 300 pounds of potassium per acre. Nitrogen in amounts up to 1,000 pounds of nitrogen per acre was disked in a short time before the corn was planted. Four inbreds and four single crosses were used. Plants were inoculated independently with *D. zeae* and *G. zeae*. The spread of rot from neither organism was affected significantly, nor was the amount of rot from natural causes affected appreciably by the various nitrogen applications. The highest nitrogen rate temporarily caused seedlings of some inbreds to turn yellow and retarded their early growth but did not affect other inbreds or crosses. In all cases, nitrogen applications caused delayed maturity of the plants, especially at the higher rates of applications, and increased stalk breaking.

So far as has been observed, soil fertility similarly affects stalk rot infection by *D. zeae* and *G. zeae*. Much, however, remains to be learned about the relation of soil fertility to stalk rot prevalence.

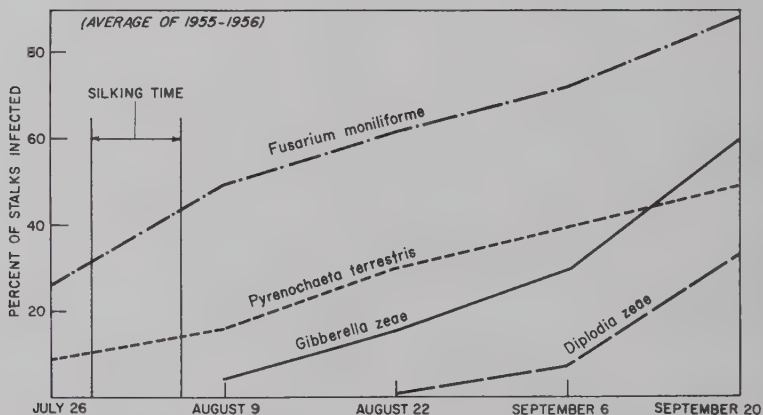
Other Influences

Not all factors that influence stalk rot development are known, but some besides those discussed have been observed. For instance, there are differences in pathogenicity among strains of the same fungus (108). Michaelson (66) found that plant infection with corn smut caused by *Ustilago maydis* (DC.) Cda. increased the susceptibility of stalks to rot by *Diplodia zeae* and *Gibberella zeae*. Infestations of second-brood chinch bugs were reported to increase the susceptibility of cornstalks to rot caused by *D. zeae* (31). That crop rotation helps some in controlling *Diplodia* ear rot has been observed (11, 50). To what extent it helps in stalk rot control is not known, but it is common knowledge that stalk rot sometimes is very damaging in areas where corn is grown intensively even when a good rotation system is followed. Nothing is definitely known about the effect of rate of planting on the amount of stalk rot, but increases in plant population do increase the tendency to stalk breaking (93).

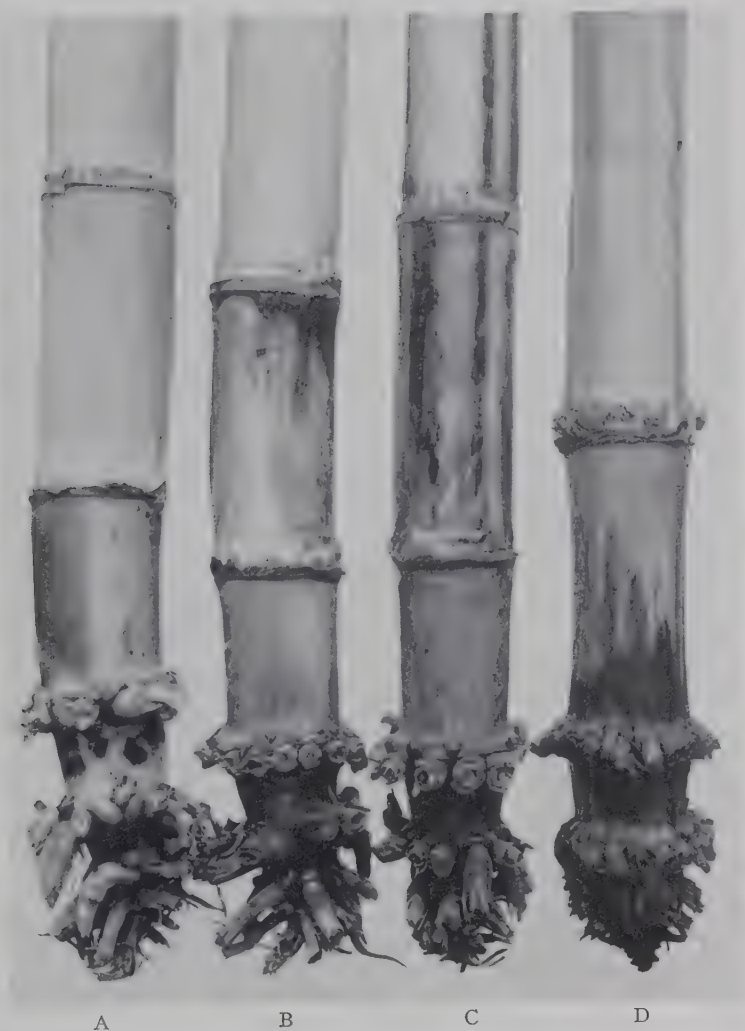
NATURAL PLACES OF ENTRY OF FUNGI INTO STALKS

In decreasing order of their economic significance, the most important natural places of entry of fungi into stalks, in a two-year test, appeared to be: (1) at the nodes through the leaf sheath junctions, (2) at root junctions above and at the ground level and, to a lesser extent, below ground, (3) through wounds made by insects, (4) directly through the stalk epidermis above and below the soil level, and (5) through shoot buds.

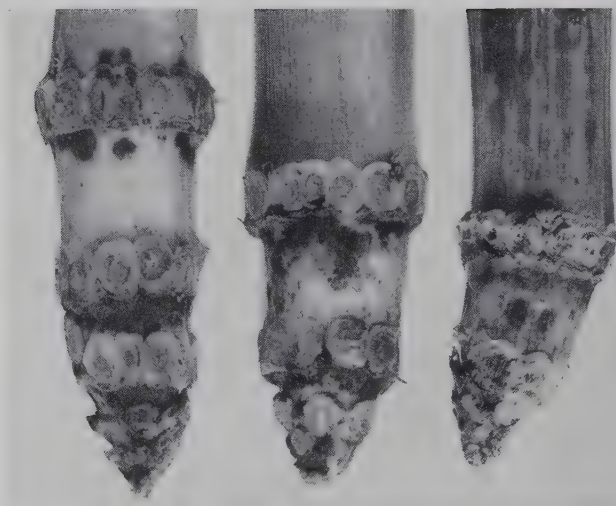
The lowermost 18 to 24 inches of cornstalks of five single crosses grown as first- and second-year corn in a rotation of corn, corn, spring grains, and clover were examined in the laboratory for the occurrence and location of lesions. The hybrids were: K4 x K201, Oh45 x C103, WF9 x 187-2, L317 x Kys, and R4 x Hy2. These were normal, thrifty plants grown in 1955 and 1956 on the Agronomy South Farm on soil that produces an average of about 100 bushels per acre. Both years, at each of the five dates indicated in Fig. 24, twelve stalks were tested from each hybrid taken from each of the two cornfields in the rotation. Some stalks, especially at the earliest dates, proved to be free from readily observable lesions; and some at the later dates were discarded because the rots had progressed too far for one to be sure of their place of origin (Fig. 25-C, D). Although the data concern only stalks having dark lesions (Figs. 1, 6, 12, 22, 26, 27),



Relative prevalence of lesions on cornstalks caused by four different fungi at five dates during the growing season. Two-year average of five hybrids, 1955-1956, Urbana, Illinois. (Fig. 24)



A, lesions at lower end of stalk caused by *Pyrenochaeta terrestris*. B and C show streaked lesions resulting from *Gibberella zeae* infection. D, rot at the base of stalk also caused by *G. zeae* but too far advanced to determine place of origin of infection. (Fig. 25)



Left, lesions caused by *Pyrenochaeta terrestris* and *Fusarium moniliforme*. A few lesions are shown immediately above the roots that had been at the soil surface, and some completely envelop the stalk surface below ground. Center, same infection but below ground only. Right, infection with *Fusarium moniliforme* through wounds made by insects. (Fig. 26)

infection not visible to macroscopic examination frequently occurred in other stalks also. Many stalks that were free from nodal discolorations and left in the laboratory for 3 days developed a mold growth at numerous nodes. *Diplodia zeae*, *Gibberella zeae*, and *Fusarium moniliforme* were commonly isolated from cuttings taken from beneath the surface of these stalks and plated in the usual way. Details about the preparation of stalks and the isolation of fungi are given under "GENERAL METHODS OF EXPERIMENTATION." As there were no consistent differences between the results from first- and second-year corn, the data have been combined.

Lesions that appeared on stalks before pollination took place were found almost entirely below or at the soil level. Some of these occurred at places where insects had fed, but most of the infections appeared to have resulted from direct penetration of the epidermis (Fig. 26). For the most part, such lesions were very shallow and apparently unimportant. Only the data obtained after pollination had taken place are averaged in Table 8 since none of the aggressive stalk rot pathogens were found before that time.

Roots originating below ground and showing discoloration from rot at the place where they emerged from the stalks were not observed until after pollination and were never numerous (Fig. 12-left). In these cases, a root or two on a stalk had rotted and then sometimes the rot had extended into the stalk, but there were no indications of a disease such as described by Whitney and Mortimore (105) which first develops as a root rot and then proceeds into the stalks, resulting in extensive root and basal stalk rot.

There is usually a whorl of roots at the ground level, which have the top side, near the stalk, exposed to the air. Here the number of stalk infections at the origin of the roots was greater than below ground. Such infection usually did not start in the root itself but at the junction of the root with the stalk. The junctions of the main brace roots with the node that bears them were also loci of this sort of infection. However, most of the infection at these nodes did not enter at those junctions, but through the connection of the leaf sheath with the node. Somewhat higher on the stalks, rudimentary roots often appeared that produced only papillae on the surface. These papillae are sometimes attacked by fungi and also serve as an entrance into the stalks (Fig. 27-right). When these loci of infection could be distinguished from those arising from the bases of leaf sheaths, they were classed under "brace roots" in Table 8.

Stalk infections originating at shoot buds were comparatively rare. The buds themselves frequently were rotted, but usually the rot did not extend into the stalks from that source (Table 8).

Rots sometimes occurred on internodes above ground, independent of a node. Spots similar to the large dark one in Fig. 22-center yielded various organisms when plated (Table 8), but the striped type



Some of the lesions shown here were the result of infection which had started through the apical end of the rudimentary brace roots. The streaked nature of some of these lesions usually indicates infection with *Gibberella zeae* (but see also Fig. 5). (Fig. 27)

of discolored area shown at the left usually yielded *Fusarium moniliforme* or bacteria or appeared to be sterile. Up to September 20, when these particular studies were terminated, no *Nigrospora oryzae* had been isolated. At other times, however, when platings were made from other types of internodal infection that are common when the corn has become mature, *N. oryzae* (Fig. 11) could be isolated consistently.

Diplodia zeae. The two years in which this experiment (Table 8) was conducted were less favorable for *D. zeae* infection than for *Gibberella zeae* (Fig. 24). The fact that *G. zeae* was found in lesions on August 9 and *D. zeae* not until August 22 is probably a variation due to seasonal conditions. Neither fungus is active as a stalk rot pathogen until after pollination, though after that, lesions caused by these two fungi continue to increase in prevalence. By far the most of the stalk infections caused by *D. zeae* occurred above ground. Most of them developed at the place of origin of the leaf sheaths (Table 8), but quite a few also developed at the junction of the brace roots with the stalks, and a smaller number developed at the origin of the roots at the soil level. Durrell (22) found the highest percentage of *D. zeae* infection at the second node above ground and then in descending order of prevalence: third, fourth, first, fifth, and sixth node. This is in general agreement with the order of prevalence observed by the writer, namely: second, third, first (origin of the main brace roots), fourth, and at the ground level. Prevalence above the fourth node was not determined.

Diplodia infections did not originate below ground as often as at any of the locations mentioned above. This is contrary to some published results (62, 63, 82), but possibly different environmental conditions obtained, and these were sufficient to cause different results. Stalk D, Fig. 25, has the appearance of a basal stalk rot that might have originated below the soil surface, but it might also have resulted from airborne spores gaining entrance at the node at the soil level. After the rot has progressed thus far, it is too late to determine the origin. In the experiments reported here, in a small number of cases Diplodia was found to have entered the stalks via roots below ground, but no stalk was found that clearly showed indications of having become infected through the mesocotyl. When routine isolations indicated the presence of active stalk-rotting fungi below ground, the stalks were split and a number of pieces were plated from the interior, including a piece from near the lower tip end which in some stalks was very dark (Fig. 15-A, C). This dark part either yielded various fungi or the plates remained sterile, but neither *D. zeae* nor *G. zeae*

was isolated. Nor were they found at the tip end of stalks such as those illustrated in Fig. 15-B or D. However, both of these stalks had been invaded by *D. zeae* or *G. zeae* down to about an inch above the lower tip, and the infection would probably have soon grown all the way down.

McNew (62) proved experimentally that *D. zeae* may enter stalks by way of the mesocotyl from infected seed or infected soil. Craig (14) proved in greenhouse experiments that *Diplodia* stalk rot may result from the addition of a copious amount of spore suspension below the soil surface eight weeks after the plants have emerged from the soil. The first lesions appeared on the roots.

Gibberella zeae. The infection pattern of *Gibberella zeae* was very much like that for *D. zeae*. Although it has frequently been thought of as more of a soil-borne fungus than *D. zeae*, the actual number of stalks infected below ground was very low, no greater proportionally than the number infected by *D. zeae* (Table 8). In only one of the classifications did it seem probable that *G. zeae* was better adapted to gain entry than *D. zeae*, and that was in the case of entry following European corn borer attack.

The course of development of *G. zeae* was studied particularly in stalks of the single cross L317 x Kys in 1957 when it was the principal cause of stalk rot at Urbana. Stalk infection started primarily at the place where the leaf sheaths were joined to the stalks. Often several lesions originated around the perimeter of a node simultaneously, and frequently there were lesions at most of the nodes from the soil level to the shank. These lesions usually enlarged downward to a greater extent than upward, but as long as the stalks were fully green, the depth of penetration into the stalks in the internodes was less than $\frac{1}{4}$ inch. As the stalks became girdled by this rot, the green color began to fade; the pith started to shrink, and longitudinal hollow areas began to develop in the stems. These hollow areas occurred first in the internodes closest to the ground and frequently appeared below the rotted area. In the earliest stages, many of these hollow areas were sterile. *G. zeae* soon invaded the spaces, however, and the lower parts of the stalks often rotted completely.

Fusarium moniliforme. This fungus was found in lesions of 26 percent of the stalks on July 26, some days before silking, and rose to 50, 61, 72, and 88 percent, respectively, on succeeding days of sampling (Fig. 24). This fungus was the most common one in all types of lesions (Table 8) except one and at all dates when collections were made in this experiment. Sometimes it was isolated independently and

sometimes in combination with other fungi or bacteria. The high prevalence of infections below the soil surface indicates that this fungus is soil borne in addition to being airborne. *F. moniliforme* was isolated from 70, 40, and 58 percent of the stalks in the first three classifications in Table 8, namely at below-ground lesions surrounding insect attacks (Fig. 26-right), on internodes below ground apparently free from physical damage (Fig. 26-center), and at the origins of discolored roots. This indicates that wounds were a factor in increasing the amount of infection. Infection was also greatly aided by growth cracks (Fig. 7). Ordinarily, however, the damage appeared to be light even though the infection percentages were high. *F. moniliforme* is a very frequent (26) parasite of cornstalks but only a moderate pathogen. It appeared to be most damaging within stalks in areas where European corn borers had been active.

***Cephalosporium acremonium*.** This fungus was isolated frequently from lesions below and above the soil surface. It was particularly frequent in discolored host tissue below and above the tunnels made by European corn borers (Table 8). It also was very prevalent in discolored tissue above and below wounds made in stalks for insertion of sterile toothpicks (Table 7, Fig. 21-C). Sometimes this fungus caused vascular discoloration to extend throughout an internode adjoining the one in which the wound had been made. *Cephalosporium acremonium* appears comparatively early. On July 26, before pollination occurred, it was isolated from lesions on 12 percent of the plants examined. All of these lesions were below the soil level. Successive examinations showed a moderate increase in the number of discolorations containing *C. acremonium*. They appeared primarily in connection with corn borer entries. However, as other fungi became more numerous, this fungus was no doubt frequently suppressed in the petri dish colonies and thus escaped detection. To obtain a full knowledge of the prevalence of *C. acremonium*, it would be necessary to consider other areas within stalks besides surface lesions and corn borer entries. This fungus is moderately parasitic in that it is able to penetrate sound tissue, but as far as stalk rot is concerned, it appears that it is a weak pathogen (1, 28, 74). Taylor (95), however, reported obtaining considerable stalk rot when using this fungus for inoculation studies.

***Pyrenochaeta terrestris*.** On July 26 about 8 percent of the stalks bore lesions caused by *P. terrestris*, and the percentage increased steadily thereafter (Fig. 24). The fungus was isolated most commonly from lesions below ground, but infections were also found as high as 8 inches above the soil surface (Table 8). The most common symp-

toms of infection were dark lesions on the internodes below the soil surface. The lesions started as small, smoky brown, circular or irregularly shaped spots (Fig. 26-left, center); as they grew older, they became larger and blacker (Fig. 12-right; Fig. 25-A). In the earlier, brown stage, these lesions could not be distinguished from those caused by *Fusarium moniliforme*, but the more advanced black stage was a distinguishing characteristic. The lesions occurring above ground had a similar color and were located at either nodes or internodes (see also page 23). The infection pattern indicates that *P. terrestris* is primarily a soil-borne parasite. Though this fungus was second only to *F. moniliforme* in prevalence, it caused very minor damage in the plants studied.

***Phaeocytospora zeae*.** This fungus was isolated most commonly from the area near the node at the soil surface. A few cases were observed on August 22 and later where *P. zeae* had entered the stalk by way of a diseased root about 1 inch below the soil surface. Most of the infection, however, was not found until the September 20 collection was made. At that time, infection had set in both below ground and up to about 8 inches above it. It was found especially at the bases of the roots occurring at the soil level. This fungus probably should be classed as a weak parasite which is both soil borne and airborne.

ARTIFICIALLY INDUCED STALK ROTS

General

Epidemics induced by artificial inoculation are useful for testing corn inbreds and hybrids for resistance to stalk rot diseases. The occurrence of natural infection is not dependable because an epidemic can not be predicted each year. Inoculation not only provides an opportunity for infection in all stalks but also provides that the infection starts at the same stage of development in each stalk.

Tests for determining resistance are made for two purposes: (a) to ascertain the resistance of established inbreds or the resistance they contribute to crosses, and (b) to facilitate selection for resistance in breeding programs. Inoculation techniques for testing have been fairly successful with *Diplodia zeae* and *Gibberella zeae* but have not been developed for other cornstalk rot pathogens.

Heald, Wilcox, and Pool in 1909 (29) were apparently the first to report inoculating cornstalks with *D. zeae*. In experiments to determine the parasitism of the fungus, they introduced it through punctures in the stalks. Smith and Holbert in 1932 (86) were probably

the first to report inoculating internodes with spore suspensions of *D. zeae* to determine the comparative resistance of different inbreds and hybrids to Diplodia stalk rot. Results from this technique were given in more detail later by Smith, Hoppe, and Holbert (87).

Age of Culture and of Spore Suspension When Used as Inoculum

The efficacy of a fungus spore suspension may be influenced by the age of the culture from which the suspension is made and by the age of the spore suspension when it is used. These variables were studied for *Diplodia zeae* inoculum used to produce corn ear rot (Table 8 in reference 50). Cultures maintained at room temperature for 105 days were very much less pathogenic than 50-day-old cultures. Those left at room temperature for 210 days depreciated still further. Spore suspensions stored at 45° F. were as pathogenic after 14 days as when freshly prepared but deteriorated appreciably in 24 days. When not refrigerated, they had become less pathogenic in 7 days and were very poor after 14 days.

During another year, *D. zeae* cultures 6 weeks old and 1 year old were compared for their ability to cause stalk rot. Some of the cultures were kept refrigerated at 45° F. after the first six weeks, but regardless of the storage temperature, the year-old cultures were worthless for inducing Diplodia stalk rot.

Diplodia cultures on cooked oats should be about six weeks old in order to have abundant mature spores for making spore suspensions. When cultures on toothpicks are used, pycnidia develop abundantly on the toothpicks in six weeks (Fig. 17). Some evidence was obtained that cultures 1 week old, that is before the spores have formed, are just as effective when inoculations are made by toothpicks (Table 11).

Table 10.—Age of *Gibberella* Culture When Used for Inoculation
Purposes (Hybrid L317 x Kys Inoculated August 11 and
Data Taken September 23, 1954)

Inoculum ^a	Age of culture when used	Internodes rotted per stalk, average
	days	number
Sterile toothpicks (check).....	..	.80
<i>Gibberella zeae</i>	8	1.32
<i>Gibberella zeae</i>	30	1.37
<i>Gibberella zeae</i>	60	1.44
<i>Gibberella zeae</i>	365	.77
L.S.D. at the 5-percent level.....	..	.21

^a Inoculum was prepared on toothpicks at various times before use and grown at room temperature.

Cultures of *Gibberella zeae* on toothpicks were inactive, too, after they were a year old (Table 10), but cultures 8 to 60 days old were pathogenic, and no difference in effectiveness was apparent within this age range. *G. zeae* inoculations, however, were at no time as effective in causing stalk rot as those of *D. zeae*. Each year several cultures were tested for pathogenicity in order to have a proved culture for the following year's work. Isolates did not always retain their pathogenicity year after year.

Stage of Plant Development When Inoculated

Michaelson (66) reported results from stalk inoculations made with *Diplodia zeae* and *Gibberella zeae* at weekly intervals from July 7 to September 8. All results were reported for the same date, September 23. *D. zeae* caused severe rot when inoculations were made July 14, several weeks before pollinating time, and at all later inoculation dates until September 1, when the grain was denting. The most severe rot occurred from the inoculations made close to pollinating time. The earlier inoculation made July 7 was much less effective even though it had the longest time to act. Three hybrids were used and all gave similar results.

There is considerable evidence that stalks do not become susceptible to natural infection by *D. zeae* until soon after pollination, and this appears to be true also when the stalks are inoculated artificially. Thus the *Diplodia* fungus that was introduced earliest was required to remain dormant for too long a time and became injured or killed by the contaminations that always enter when inoculations are made, or it may have been injured by other causes (66).

The results from inoculating with *G. zeae* (66) at different times were more erratic, but the inoculations were most effective when they were made August 4 and 11, presumably about pollinating time and a week later.

Hooker (33) made stalk inoculations with *D. zeae* in five dent corn inbred lines at intervals of 1, 2, 3, and 4 weeks after silking. In all cases records were made at weekly intervals until the fourth week after inoculation. The earliest inoculation averaged a slightly greater spread of rot than did the inoculations made later. Rot in susceptible inbreds continued to spread week after week, but in the resistant inbred B14, the rot made little progress after the first week.

Some experiments were conducted in Illinois to determine the effect of the age of plants on the efficacy of stalk inoculation. Data on three inbreds and three dates of inoculation are presented in Table 11.

The examinations were also made at different dates (Table 11) which were coordinated with the times of inoculation. Ky27 was chosen because of its known susceptibility to damage from natural infection with *Gibberella zeae* (Fig. 20). K201 was included because of its exceptional character of being resistant to natural infection by *D. zeae* and *G. zeae* but highly susceptible when inoculated (see also Table 1). The inbreds varied in their times of silking. Ky27 and P8 usually silked at about the same time, but in this case, Ky27 was slightly earlier. K201 silked about two weeks later than Ky27 (Table 12).

For both fungi, inoculation a few days before silking was as effective as at any other date, but inoculations with *D. zeae* on K201 three weeks before silking gave poor results as compared with later inoculations. Ky27 developed significantly less rot from *D. zeae* and *G. zeae* when inoculations were made as late as August 18, which was about four weeks after silking. With inbred P8, however, none of the differences in amount of rot was significant for the different stages of plant

Table 11.—Average Number of Internodes Rotted and of Prematurely Dead Plants in Three Corn Inbreds Inoculated With *Diplodia zeae* and *Gibberella zeae* by the Toothpick Method at Three Stages of Plant Development,^a Urbana, 1954

Corn inbred	Fungus used for inoculation	Internodes rotted per stalk, average			Prematurely dead plants		
		Inoc. July 15 ^b	Inoc. Aug. 4 ^c	Inoc. Aug. 18 ^d	Inoc. July 15 ^b	Inoc. Aug. 4 ^c	Inoc. Aug. 18 ^d
		number	number	number	angle	angle	angle
Ky. 27.....	None ^e	.59	.69	.62	4	17	19
	<i>Gibberella</i> ^f	1.47	1.29	1.08	21	28	29
	<i>Diplodia</i> ^g	2.51	2.38	2.00	40	48	50
	<i>Diplodia</i> ^h	2.76	2.35	2.11	42	50	55
Ind. P8.....	None ^e	.38	.70	.80	0	0	3
	<i>Gibberella</i> ^f	1.31	1.18	1.13	0	0	5
	<i>Diplodia</i> ^g	2.43	2.20	2.45	0	0	27
Kan. K201..	None ^e	.41	.97	.75	0	0	0
	<i>Gibberella</i> ^f	2.01	2.24	1.93	0	0	18
	<i>Diplodia</i> ^g	2.33	4.03	4.04	2	21	28
L.S.D. at the 5-percent level ⁱ		.31	.31	.31	6	6	6

^a For information on plant development, see Table 12.

^b Examined September 9.

^c Examined September 16.

^d Examined September 22.

^e Sterile toothpicks inserted in the same manner as for the fungus inoculations.

^f Cultures 2 weeks old, very few spores, exposed to daylight.

^g Mycelium and numerous spores, cultures 6 weeks old, exposed to daylight.

^h Mycelium only, cultures 1 week old.

ⁱ The same L.S.D. also applies between dates.

Table 12.—Stages of Development of Plants on Which Data Are Reported in Table 11

Corn inbred	Date inoculated	Stage of development when inoculated
Ky. 27.....	July 15 August 4 August 18	Starting to tassel, no silks Silks all out, some turning brown Late milk stage
Ind. P8.....	July 15 August 4 August 18	No tassels or silks showing Silks all out, a few turning brown Late milk stage
Kan. K201.....	July 15 August 4 August 18	No tassels or silks showing 50 percent in silk Milk stage

development at the time of inoculation. In general, for all three inbreds and both pathogens, the inoculation that was closest to the time of silking tended to be the most effective. Inoculations made two weeks later resulted in a significant reduction in the spread of rot in two cases but not in any significant reduction in five others.

Further data on the relationship of plant development to the spread of *Gibberella* rot are given in Table 13. These results substantiate the conclusion given above. All the data reported agree that the timing for the best results from stalk inoculations is not critical. Thus if a number of inbreds or hybrids are to be rated for resistance to *Diplodia* or *Gibberella* stalk rot, and they differ up to 10 days in time of silking, all the inoculations can be made at the silking time of the latest entry. If the results are to be measured by the spread of rot, all of the plants can be examined at the same time, but if the results are to be measured in terms of premature dying, records should be made at different times, perhaps at equal time intervals after silking.

Table 13.—Development of Plants in Relation to Spread of *Gibberella* Rot: Cornstalks Were Inoculated With *G. zeae* by the Toothpick Method at 2-Week Intervals (All Results Measured September 29) Hybrid U. S. 13, Urbana, 1953

Date inoculated	Growth development of plants	Average number of internodes rotted per stalk
July 23.....	Shortly before silking	1.18
August 4.....	About 1 week after silking	1.06
August 18.....	A few kernels denting slightly	.97
September 1.....	Grain moisture 44 percent	.44
L.S.D. at the 5-percent level..		.19

Choosing the Internode to be Inoculated

The first internode above ground is shorter than the others (Figs. 2, 3, 5, 25), is often enveloped by the brace roots, and is more difficult to split open. Thus for various reasons it is not convenient for inoculation purposes. The second internode above ground is referred to below as the first elongated internode. Ordinarily this is also the first internode above the main brace roots.

Working with 4 inbreds, Hooker (33) made inoculations with *Diplodia zeae* in the first, second, third, fourth, and fifth elongated internodes of different plants. He found that the height above ground of the internode inoculated made a difference in results in comparatively resistant inbreds. In the resistant B14, the rot was least in the first and second elongated internodes and increased progressively in the next three internodes, so that in the fifth internode, the rot was just as severe as in the susceptible Os420. In Os420, the rot was equally severe in all internodes inoculated.

In Illinois, inoculations were made in the first, third, and fifth elongated internodes in replicated plots of hybrid U.S. 13. Inoculations were made at silking time and readings were made six weeks later. In this case, inoculations with *D. zeae* produced about the same amount of rot in each internode inoculated (Table 14). The results were the

Table 14. — Relation Between Which Internode Was Inoculated and the Average Number of Internodes Rotted per Stalk, Urbana

Inoculum	Year	Hybrid	Method of inoculating	Height of internode above main brace roots	Internodes rotted per stalk
<i>Gibberella zeae</i>	1953	U.S. 13	Toothpicks	first	1.50**
				third	.97**
				fifth	.90
<i>Diplodia zeae</i>	1953	U.S. 13	Inoculator	first	2.68
				third	2.65
				fifth	2.47
<i>Diplodia zeae</i>	1954	U.S. 13	Inoculator	first	2.93
				third	2.89
				fifth	2.69
<i>Diplodia zeae</i>	1957	Ill. 1570	Inoculator	first ^a	1.23*
				fourth	1.44*

^a In this year, 1st and 4th internode inoculations were both made in the same stalks. In other years only one inoculation was made per stalk.

* Difference significant at the 5-percent level.

** Difference significant at the 1-percent level.

same for two years. In a one-year test with *Gibberella zeae*, significantly more rot occurred in the first elongated internode than in the third or fifth (Table 14). On the other hand, Cappellini (9) obtained opposite results in a one-year test in New Jersey. He made inoculations with *G. zeae* in the first, second, third, and fourth elongated internodes of four inbreds and obtained increasingly greater amounts of rot with distance up the stalk.

In 1957 inoculations were made with *D. zeae* in the first and fourth internodes of the same plants of hybrid Ill. 1570. This time, the higher point of inoculation had significantly more rot (Table 14). This might indicate that a rot low on the stalk affects the susceptibility of the stalk above that area, or in this case the stalks might have been more susceptible at the higher location, as reported by Hooker, regardless of double inoculation.

The possible relationship between the susceptibility of different internodes and their carbohydrate content has also been investigated.¹ In work performed by DeTurk *et al.* (16) in 1935, two single crosses had consistently lower total active carbohydrates and lower total sugars in the lower part of the stalks than in the middle parts regardless of whether the plants were normal or whether the leaves had been partially defoliated. This might indicate greater susceptibility in the lower part of the stalks. In 1936, however, (17) using the same single crosses and techniques, they found that this situation was true only when leaves had been pruned. The lowest total sugar content now was found, in normal plants, to occur in the middle part of the stalk. Growing conditions, time of sampling, and inbreds or hybrids used, could all possibly make a difference in the relative amounts of sugar in different parts of the stalks, with related differences in susceptibility.

Since most natural rot takes place in the lower part of the stalks, if only one inoculation is made per plant, it would seem advisable to inoculate no higher than the second internode above the main brace roots (10 to 15 inches above ground). This will best show the differences in susceptibility between different kinds of corn. However, multiple inoculations with the same organism also should be considered. In this case, perhaps three inoculations in alternate nodes should be made. Under conditions favorable for rot development, considerable premature dying may take place in susceptible corn (Tables 1 and 3), eliminating the necessity of cutting stalks open.

¹ For a discussion of sugar as a factor in stalk susceptibility, see "Nature of resistance," page 48.

Technique of Inoculation

Diplodia zeae. Two methods of inoculating cornstalks with *D. zeae* have been widely used. In the first, a spore suspension is injected with an inoculator (2, 32, 40, 44, 45, 84, 87, 97). In the second, a culture of the fungus growing on toothpicks is inserted into previously made openings in the stalks (18, 66, 107, 111). Pipestem cleaners soaked in a spore suspension and inserted into stalks (27, 68, 103) have also been used sometimes (see "General Methods of Experimentation," page 28). In this investigation, the results from these three methods of inoculation were compared by four methods of measurement (Table 15). The results varied somewhat according to the method of measurement, but the differences were not significant. The inoculator gave as good results as the other methods tried. In contrast to this, Williams and Menon (106) found that inoculations made with a hypodermic syringe (inoculator) caused less rot than any of three other methods and that the toothpick method was decidedly the best. However, there is no information about the spore concentration of the spore suspension they used. It is known that differences in concentration influence the amount of rot when the inoculator is used. Furthermore, Williams and Menon made their stalk inoculations in the internode above the ear-bearing node, while the inoculations reported in Table 15 were made in the second internode above the main brace roots.

Table 15.—Inoculation Methods Using *Diplodia zeae*: A Comparison of Three Methods of Inoculation and Four Methods of Measuring Results (Hybrid U. S. 13 Inoculated in the Second Internode Above the Main Brace Roots) Urbana, 1950

Inoculum	Method of inoculating	Plants with major leaf surface dead Sept. 27	Plants with leaves and stalks dead Oct. 10	Diplodia pycnidial development Oct. 10	Internodes rotted per stalk Oct. 10
		<i>perct.</i>	<i>perct.</i>	<i>score</i>	<i>number</i>
None.....	None	14.8	25.2	.39	
None.....	Sterile toothpicks	16.4	30.8	.35	.77
Sterile water.....	Inoculator	17.6	27.8	.43	.68
Sterile water.....	Pipestem cleaners	20.2	32.8	.49	.74
<i>Diplodia zeae</i>	Toothpicks	38.0	72.8	1.28	1.82
<i>Diplodia zeae</i>	Inoculator	35.6	61.6	1.46	2.05
<i>Diplodia zeae</i>	Pipestem cleaners	40.0	72.2	1.59	2.04
L.S.D. at the 5-percent level.....		12.1	13.6	.36	.25

The inoculator method using spore suspensions is satisfactory only for fungi that produce spores abundantly in culture.

***Gibberella zeae*.** A number of methods of inoculating with *G. zeae* have been reported. Toothpick cultures have frequently been used (18, 66, 111) and some investigators have made holes in stalks in which agar culture (106) or culture on whole grains of wheat (84) or barley (32) was inserted. The latter method had also been used by P. E. Hoppe (personal communication). Others used the pipestem cleaner method (27, 68, 103). As *G. zeae* isolated from corn usually sporulates poorly on agar medium, the inoculator method is usually not effective, although Williams and Menon (106) reported using it successfully. Some cultures of *G. zeae* do sporulate abundantly but care must be taken to make sure they are pathogenic. A suspension of a finely ground culture of *G. zeae* grown on wheat, strained, and used with an inoculator has also been tried (84).

Experiments were conducted at Urbana using three methods of introducing *G. zeae* inoculum into the second elongated internode of stalks of two single crosses. A culture on cooked oat kernels was used by inserting a single kernel into a small diameter hole made with a cork borer and then closing the hole with surgical tape. This was compared with the toothpick and pipestem cleaner methods. Results were measured in terms of number of internodes rotted and the percent of prematurely dead plants (Table 16). There were no significant differences between any of the methods of inoculation. On the average, the toothpick method gave as satisfactory results as any and

Table 16.—Progressive Development of *Gibberella* Stalk Rot in Two Hybrids: Inoculations With *Gibberella zeae* Were Made by Three Methods About Six Days After Silking, Urbana, 1950

Inoculum	Method of inoculating	Average number of internodes rotted per stalk when examined on different dates ^a						Percent dead plants ^b	
		Hybrid 38-11 x L317 ^c			Hybrid K4 x Kys ^d			38-11 x L317	K4 x Kys
		Sept. 15	Oct. 5	Oct. 20	Sept. 18	Oct. 8	Oct. 24	Oct. 20	Oct. 24
None (check).	Toothpicks (sterile)	.42	.75	1.22	.72	.85	.95	56	14
<i>G. zeae</i>	Toothpicks	.68	.92	2.14	.94	.98	1.14	77	17
<i>G. zeae</i>	Pipestem cleaners	.53	.96	1.84	.87	1.08	1.15	70	16
<i>G. zeae</i>	Oat kernels	.81	1.06	1.57	.93	.97	1.11	62	18

^a Differences in results between dates highly significant. Differences between the check and the inoculated stalks significant but differences between methods of inoculation not significant.

^b Differences between hybrids highly significant. Differences between the check and the inoculated stalks significant but differences between methods of inoculation not significant.

^c Nearly full silk, August 2; inoculated, August 8.

^d Nearly full silk, August 5; inoculated, August 11.

was the simplest one to use in making inoculations in the field. The inoculator was not used because it requires a higher concentration of spores than that obtained from the *Gibberella* cultures used.

Artificially induced infections with *G. zeae* are less pathogenic than those of *D. zeae* although natural infections of *G. zeae* are often just as virulent. The reason for this is not known.

Plants were also inoculated by inserting inoculum into one of the lower nodes, but this produced about the same results as internodal inoculations.

***Fusarium moniliforme*.** Several workers have reported making successful stalk inoculations with *F. moniliforme* by inserting a piece of agar culture of the fungus into a hole made with a cork borer (24, 57). As this fungus sporulates profusely, any of the methods described ought to work well.

Mixed cultures. Attempts have been made to test for resistance to several diseases at the same time by use of a mixture of fungus inoculum (27, 68). Michaelson (66) found that when he inoculated with *Diplodia zeae* and *Gibberella zeae*, using separate toothpick cultures but inserting the toothpicks side by side, the extent of rot was no different than when *D. zeae* alone was used. In other words, when two pathogens were used together the result was about the same as when the more virulent one was used alone.

Measuring Results From Inoculations

When to determine results. Various investigators have used different time periods between making inoculations and recording results. These have ranged from 12 to 14 days (106) to 8 or more weeks (88). Hooker (33) made observations at 1-week intervals up to 4 weeks and concluded that records should be made at least 3 weeks, and preferably 4 weeks, after inoculation. At Urbana two single crosses were inoculated with *Gibberella zeae* about one week after silking and records were made 38, 58, and 73 days after inoculating, that is within a range of approximately 5 to 10 weeks (Table 16). At the first reading, K4 x Kys was the more susceptible, but at the last reading, 38-11 x L317 had the most rot which had spread from the inoculation point. This was true for all three inoculation methods. This shift also occurred in the toothpick-treated checks. This reversal in results was probably an effect from the large percentage of dead plants in 38-11 x L317 at the last date. More than half the plants were dead in the checks, and so at that time dying was to a large extent the result of

causes other than inoculation. Apparently premature dying accelerated the rotting induced by the inoculations.

Records should be made not sooner than 3 or 4 weeks after inoculation and can be made later than that, but should be made before the check plants begin to die as a result of maturity. Furthermore, if it is desired to measure only the effect of artificial inoculation, then the results should be determined before the check plants die from natural disease infection.

Reisolation of the fungus. There is little doubt that when a vigorous rot takes place from inoculations with *Diplodia zeae*, that this fungus has been the cause. With *Gibberella zeae* and other fungi, however, it is well to make reisolutions to determine whether the fungus used as inoculum was actually the cause of the rot. Even injecting sterile toothpicks in the same manner as when making inoculations can result in a considerable amount of rot (Fig. 21) which yields a high percent of *Fusarium moniliforme*, of *Cephalosporium acremonium* (Table 7), and of bacteria.

Area involved by rot. Various means have been used for recording the extent of rot as seen when the cornstalks are split open. DeVay *et al.* (18) used four classes, called (R), (MR), (MS), and (S), which were based on whether less than $\frac{1}{4}$ of an internode was discolored, $\frac{1}{4}$ to $\frac{1}{2}$, $\frac{1}{2}$ to $\frac{3}{4}$, or more than $\frac{3}{4}$. Hooker (32) used ratings based on the same divisions of the internode, plus a class for infection extending into adjoining internodes, and a class for plants killed. A third method, used by the writer and by some others (44, 111), is to record the number of internodes rotted, using decimals to indicate the extent of rot within or extending beyond one internode. Thus the rots in Fig. 21-right for the 6 stalks of Ky27 x 38-11, reading from left to right would be about 1.1, 1.7, 1.1, 1.0, 0.2, 0.1. The area of the rot in relation to the internodes was considered rather than simply the length of the rotted area. This method is probably best adapted when records are made more than 3 or 4 weeks after inoculation.

Prematurely dead plants. Stalk inoculations, particularly with *D. zeae*, cause more premature dying than occurs from natural infection (Tables 1, 6, 11, 15), and this information in itself may be a good basis for determining susceptibility. (For the limitations of the method, see page 36.) Multiple inoculations (Table 3) hasten the premature dying of susceptible plants, allowing a greater margin of time between the periods of premature dying from stalk rot and natural dying from maturity. However, this method is not very dependable in regions where early frosts occur.

Dependability of Results

A high correlation has been reported (32, 42, 87) between the penetration of the stalk by rot from internodal inoculations and the amount of rot which results from natural infection. If this is usually true, then susceptibility to artificial infection is a reliable sign of susceptibility to natural infection. On the other hand, Semeniuk (80) and Semeniuk *et al.* (84) found that spread of rot from *Diplodia zeae* inoculations did not correlate with the amount of rot that was caused in 1938, 1939, and 1940 by natural *Diplodia* infection of inbreds and hybrids. Sprague (88), however, reported that in the corn breeding work in Iowa, good progress has been made in obtaining better resistance to stalk rots by the use of stalk inoculation.

In Illinois, the spread of rot from artificial inoculation with *Gibberella zeae* and *D. zeae* (Table 1) was correlated with premature death from natural causes. The correlation with the check rows was at the 1-percent level for *G. zeae* and at the 5-percent level for *D. zeae*. The 5-percent level is significant, and the 1-percent level is highly significant.

The amount of rot occurring from natural infection with *G. zeae* also correlated highly with the percentage of prematurely dead plants but did not correlate significantly with the spread of rot resulting from inoculation with the same fungus. The amount of rot from natural infection with *D. zeae* (Table 1, Column H) was correlated at the 5-percent level with the spread of rot due to inoculation with this fungus, and to a lesser extent the incidence of natural *D. zeae* rot correlated with the incidence of prematurely dead plants in the check rows. The infection there was caused primarily by *G. zeae*.

The greatest discrepancy between response to natural infection and response to artificial inoculation was found in the single cross 38-11 x K201 (Table 1), and more specifically in the inbred K201 (Table 11). The exceptional reaction to artificial inoculation of this inbred by itself or in crosses is a good example of how results from inoculation may be misleading. It had been fairly resistant to *D. zeae* and *G. zeae* as judged by the extent of natural infection or of premature death of plants, but in tests at Urbana it was very susceptible to rot by both of these fungi when they were introduced artificially. If data from this cross were omitted from Table 1, the correlations referred to above for the other 8 hybrids would be significant.

Another interesting inbred is Ky27. Zuber *et al.*, working in Missouri (111), found this inbred resistant as judged by artificial inoculation with *G. zeae*, but in Illinois, it has been very susceptible to

natural infection (Fig. 20). Similarly, the high susceptibility of inbred R4 to *Diplodia* stalk rot was not discovered from stalk inoculation tests (42, Tables 14, 15) (43, Table 3 in appendix) but was obvious in the natural *Diplodia* epidemic of 1938 and at various times since then.

Results from artificial inoculation have not agreed with extent of rot caused by natural infection when the leaf area has been reduced by pruning (see Leaf Damage, page 53).

There is evidence (42) that reaction to stalk rot is influenced by the environment during the growing season and that not all inbreds or hybrids react similarly to changes in environment. Thus in some cases an inbred may be comparatively resistant in one test and comparatively susceptible in another. Nevertheless, in certain tests the spread of rot induced by inoculation has been consistent among inbreds and hybrids during successive years (32, 84).

Another type of consistency also was found in experiments performed in Illinois. A spore suspension of *D. zeae* was inoculated into the first and fourth internodes above the main brace roots of the double-cross hybrid Ill. 1570. The spread of rot varied among the 96 plants in the test, but there was an association, significant at the 1-percent level, between the extent of rot from the two inoculations within each stalk. This signifies that the results from the inoculation technique were precise enough to permit determining differences in susceptibility between stalks of the same hybrid.

Stalk inoculation is now considered to be a generally reliable means of facilitating selection for resistance to stalk rot. The cases where the results are misleading certainly appear to be exceptions rather than the rule.

CONTROL MEASURES

Cornstalk rot diseases can not be controlled satisfactorily at the present time, but damage can be reduced by giving attention to certain details. The following statements apply primarily to *Diplodia* and *Gibberella* stalk rot, which usually cause the most stalk rot in Illinois. Most generally, resistance to *Diplodia* and *Gibberella* stalk rot seems to be associated, but there are exceptions.

Limited tests of available hybrids (71, 72, 73) have established that different hybrids vary greatly in their susceptibility to stalk rot and that the differences in susceptibility have, in general, been consistent when the same hybrids were compared at different locations and for different years (Table 2).

Varieties which mature early in a given region should be avoided because they are more susceptible there than where they are full-season varieties.

The development of resistant hybrids depends on the production of more resistant parent lines, but this is not easily accomplished because there is some association between high yield and susceptibility (Table 4).

Leaf blights increase the susceptibility of corn plants to stalk rot. Some definite accomplishments have been achieved in breeding for resistance to *Helminthosporium* and Stewart's blight (38, 49), and some blight-resistant inbreds are now generally available. Their use will aid in reducing stalk rots, but severe rot damage has occurred on many farms even in the absence of leaf blight infection.

Soils that contain a large amount of organic matter and available nitrogen are likely to have a high incidence of stalk rots in susceptible hybrids. This condition has generally been found to be most acute in soils in which the potassium content was low. Insufficient phosphorus also has been observed to increase disease incidence, although to a less extent. But phosphorus should not be neglected, even though its deficiency appears to have only a minor effect on stalk rot, because the soil must have adequate phosphorus to produce good yields.

Large amounts of nitrogen fertilizers may require large amounts of muriate of potash for balanced nutrition and stalk rot control. Stalk rot control appears particularly to be furthered by the chlorine contained in muriate of potash (110). Adequate potassium is residual in some Illinois soils but needs to be applied to others.

A high fertility program in itself may increase stalk rots, particularly after the program has been in operation for a number of years. Since, however, stalk rot also depends on other factors, the susceptibility caused by high fertility does not lead to the same amount of rot at all locations or to the same amount year after year. To overcome the susceptibility that is induced, hybrids must have a high degree of inherent resistance to rot diseases and enough mechanical strength to sustain the effect of whatever rot occurs.

Crop rotation helps to control both diseases and insects. Use of soybeans may help considerably in the rotation as, in general, organisms causing serious diseases in corn do not attack soybeans and vice versa. Good rotations that include a sod crop also keep the soil in a better state of tilth, which will mean better aeration and less likelihood of root rot.

It has not been determined whether thick planting actually increases the development of stalk rots, but thick planting in itself reduces the

mechanical strength of stalks, and stalk rots also weaken the stalks. Thus the two together may greatly increase stalk breakage.

When *Diplodia* and *Gibberella* spores were fed to cattle, the *Diplodia* spores were not viable when recovered and the *Gibberella* spores were not recoverable (91). They apparently had been digested.

SUMMARY

Ten different stalk rot diseases are described and illustrated. Discussions of experimental work are confined largely to rots caused by *Diplodia zeae* and *Gibberella zeae* because, as a rule, they are the most important stalk diseases in Illinois. The other eight diseases, in the order in which they are discussed, are: *Fusarium*, Charcoal, Bacterial, and *Pythium* stalk rot and *Nigrospora*, *Phaeocytospora*, *Pyrenochaeta*, and Stewart's disease stalk infection.

Five different methods of measuring the amount or effect of stalk rots for use in determining comparative prevalence are discussed. They are: prematurely dead plants, broken stalks, firmness of stalks, surface discoloration, and internal discoloration. These differ more or less in principle, and none of them is perfect, but in general there has been a good correlation between the results obtained between any two of them. However, the ratings of some inbreds or hybrids differed significantly under different methods of measurement. Some of these inbreds and hybrids had less lodging than average even though the amount of rot was above average, and some died quickly even though the amount of rot in them was not as high as in others that remained green. Furthermore, some were susceptible when inoculated although they had rated as resistant to natural infection. The opposite situation also occurred.

When stalk rot damage was above average, a negative correlation was obtained between stalk rot severity and yield in all but 1 of 15 hybrid corn tests conducted over a period of years. Most of these correlations were highly significant. Actual losses in yield were also determined in these tests. The average difference between the ten hybrids with lowest score for stalk rot in each test and the ten with the highest score in the five most recent large-scale tests was 10 bushels per acre.

Eight factors influencing natural rot development are discussed. Weather conditions and inherited resistance appear to be the most important of the variables influencing the prevalence of stalk rots. Data are presented to show that susceptibility to *D. zeae* and *G. zeae* is associated with the ability to produce high yields. Earliness was

associated with susceptibility, even though differences in the time to reach maturity were small. Premature partial loss of green leaf area, regardless of the cause, increased susceptibility to rot produced by *D. zeae* and *G. zeae*. On the other hand, the rot associated with infestation by the European corn borer was produced mainly by *Fusarium moniliforme*. Unbalanced soil fertility was always conducive to stalk rot. This was especially apparent when it involved low potassium and high nitrogen. Under some conditions, high fertility by itself had the same effect.

Investigations were conducted for two years with regard to the natural places parasitic fungi enter cornstalks. At about a week before silking time, dark lesions on the stalks were found primarily below the soil surface and were caused principally by *F. moniliforme* and *Pyrenochaeta terrestris*. A few small lesions caused by *F. moniliforme* occurred above ground at pollinating time, and lesions caused by *D. zeae* and *G. zeae* appeared soon thereafter. Lesions caused by all four of these fungi continued to increase in number and generally also in size until the last examination, September 20. The largest number of infections caused by *D. zeae* and *G. zeae* occurred at the nodes above the soil surface. Relatively few infections by these fungi started below ground.

The prevalence of Diplodia and Gibberella stalk rot as a result of natural infection appeared to depend very little on physical wounding. The prevalence of discolorations caused by *F. moniliforme* and *cephalosporium acremonium*, however, was considerably greater in stalks having wounds than in unwounded stalks.

Most of the *D. zeae* culture used for inoculum on toothpicks was about 6 weeks old, but even 1-week-old culture was satisfactory for the toothpick technique. *G. zeae* cultures 8 to 60 days old were nearly equally effective when grown on toothpicks. If cultures of *D. zeae* or *G. zeae* were kept a year, they become impotent. Refrigerated spore suspensions of *D. zeae* were good for 14 days, but when such suspensions were not refrigerated, they were fully active for only a few days at midsummer temperatures.

Cornstalks of the same inbred or hybrid sometimes have reacted differently when artificially inoculated at various heights above the ground. As rot from natural infection occurs most extensively in the lower part of the stalk, it is suggested that inoculations be made about 12 to 15 inches above the soil in case of single inoculations. Multiple inoculations in alternate internodes with the same inoculum, particularly *D. zeae*, may allow the recording of premature dying of plants as a satisfactory criterion of resistance.

Ratings for susceptibility as determined by stalk rot initiated by artificial inoculations have not always agreed closely with ratings obtained during a natural epidemic of the disease. However, when considerable numbers of corn entries were involved, the correlations between results from the two modes of infection were usually good, and artificial inoculation therefore appears, for the most part, to be a dependable means for determining resistance. It provides infection at will, whereas the occurrence of natural infection is unpredictable.

Stalk rot diseases can be checked, but they can not be entirely controlled. Since hybrids differ in resistance, the use of the more resistant ones is recommended. Under present tendencies toward higher soil fertility, higher plant populations, and more intensive cropping, breeding for better resistance is needed. Balanced soil fertility, particularly with respect to adequate potassium as indicated by tests, is important. Hybrids that utilize the full growing season are usually less susceptible to stalk rot than those that mature a little earlier. Crop rotation, moderate rates of planting, and avoidance of excessive use of fertilizers can be expected to help to some extent in reducing stalk rot damage.

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